

THE NATURAL  
HISTORY OF  
PLANTS





22102021744

Med  
K4975





THE  
NATURAL HISTORY OF PLANTS

THEIR FORMS, GROWTH,  
REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF  
ANTON KERNER VON MARILAUN

PROFESSOR OF BOTANY IN THE UNIVERSITY OF VIENNA

TRANSLATED AND EDITED

BY

F. W. OLIVER, M.A., D.Sc.

QUAIN PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON

WITH THE ASSISTANCE OF

MARIAN BUSK, B.Sc. AND MARY F. EWART, B.Sc.

WITH ABOUT 2000 ORIGINAL WOODCUT ILLUSTRATIONS AND SIXTEEN PLATES IN COLOURS

---

DIVISIONAL VOLUME IV.

---



LONDON: BLACKIE & SON, LIMITED  
GLASGOW, EDINBURGH, AND DUBLIN

WELLCOME INSTITUTE LIBRARY	
Coll.	welMOMec
Call	
No.	01

# CONTENTS OF DIVISIONAL VOLUME IV.

## LIST OF ILLUSTRATIONS.

	PAGE
PLATE IX. MOSSES AND LIVERWORTS.—Drawn by Ernst Heyn, - - - - -	to face 66
„ X. ALPINE RHODODENDRONS AND MOUNTAIN PINES (TYROL).—Drawn by Ernst Heyn, - - - - -	106
„ XI. VICTORIA REGIA IN THE RIVER AMAZON.—Drawn by Ernst Heyn, - - -	184
„ XII. ALPINE FLOWERS IN THE TYROL.—Drawn by Ernst Heyn, - - -	198
„ XIII. WEST INDIAN ORCHIDS ( <i>Stanhopea Devoniensis</i> and <i>Oncidium Papilio</i> ).—Drawn by Ernst Heyn, - - - - -	224
<i>Illustrations in the Text—Fig. 189 to Fig. 295.</i>	

## INTRODUCTION.

	Page		Page
Sources of a History of Plants, - - - - -	1	The Language of Botanists, - - - - -	3

## THE GENESIS OF PLANT-OFFSPRING.

1. ASEXUAL REPRODUCTION.		Protection of Pollen, - - - - -	104
Spores and Thallidia, - - - - -	8	Dispersion of Pollen by the Wind, - - -	129
Buds on Roots, - - - - -	25	Dispersion of Pollen by Animals, - - -	152
Buds on Stems, - - - - -	28	Allurements of Animals with a View to the Dispersion of Pollen, - - - - -	167
Buds on Leaves, - - - - -	37	The Colours of Flowers as a means of Attracting Animals, - - - - -	182
2. REPRODUCTION BY MEANS OF FRUITS.		The Scent of Flowers as a means of Attracting Animals, - - - - -	198
Definition and Classification of Fruits, - - -	46	Opening of the Passage to the Interior of the Flower, - - - - -	209
Fertilization and Fruit-formation in Cryptogams, - - - - -	49	Reception of Flower-seeking Animals at the Entrance to the Flower, - - - - -	221
The Commencement of the Phanerogamic Fruit, - - - - -	70	Taking up of Pollen by Insects, - - - - -	243
Ovaries on a Conical Receptacle, - - - - -	75	Deposition of Pollen, - - - - -	276
Ovaries on a Flat or Excavated Receptacle, - - -	76	The Crossing of Flowers, - - - - -	287
Stamens, - - - - -	85	Autogamy, - - - - -	331
Pollen, - - - - -	95		



# THE NATURAL HISTORY OF PLANTS.

---

## INTRODUCTION.

Sources of a History of Plants.—The Language of Botanists.

### SOURCES OF A HISTORY OF PLANTS.

FROM the sixteenth to the latter part of the eighteenth century, "*Historia plantarum*" was the customary title for botanical works. Most of the scholars of that time took as their authorities and models the writings of Theophrastus, the celebrated pupil of Aristotle, together with the thirty-seven books constituting Pliny's "*Historia naturalis*". Thus it came about that the titles of the new books were similar to those of Theophrastus and Pliny. However, all these books are anything but histories of plants, if in the idea of a history we include an account of the changes which occur within the limits of space and time. In reality the bulky folios of Clusius, Bauhin, and Haller, the title-pages of which bear the inscription "*Historia plantarum*", contain descriptions merely of the external characters of plants, accompanied by only sparing details of the situations in which these plants had been found growing wild. Works of this kind, dealing with limited areas of country, were later on distinguished by the name of Floras. By this name they are still known.

Although the authors of the Flora had no such purpose in view, their works furnished the starting-point for a real history of the vegetable world. A comparison of the Floras of neighbouring regions shows that certain plants inhabit a greater, others a lesser area; that the boundaries of the species confined to a distinct district coincide with territories inhabited by various races of mankind; that the boundaries of this and that species coincide and stand in relation to various climatic and other conditions.

All plants have the power of propagating themselves. They send their offspring forth as colonists towards all points of the compass, and endeavour in this way to enlarge their areas of distribution. Suppose that a species hitherto subsisting in localities where there are seven months of snow and five months of vegetation in the year multiplies, and that its descendants are scattered in all directions, what would happen if any of these emissaries reached places where frost and snow

prevail for eight months instead of seven, and where the season for vegetation is confined to four months? They would succumb to the inhospitality of the climate; and it follows that a limit to the distribution of the species in question would be attained at a line connecting all places which possess a climate of equal rigour. This does not preclude the possibility of other causes constituting a barrier to the distribution of the same species in other directions. Peculiarities of soil, for instance, may prevent the naturalization of a plant; or, its spread may be baffled by the opposition of plants already long settled in the place invaded; or any other like impediment may operate as a check. Facts of this kind, being brought to light by the comparison of different Floras, led to detailed research into the means of reproduction and distribution in plants, to a study of the many contrivances for their propagation, and of the nature of the equipments which enable the descendants of a stock to enlarge the area where it grows.

Side by side with these investigations into the history of individual kinds of plants, there was developed a special department of research with the view of determining the actually-existing boundary-lines of distribution—the so-called lines of vegetation—of particular species, and of ascertaining all the conditions of soil and climate affecting plant-life which prevail along these lines, so as to take into consideration all the possible causes of limits to distribution. The range of observations was likewise extended to displacements of the lines of vegetation, to the advance of particular species in one direction or another, and the suppression and annihilation of others within historic times; thus a chronicle of plant migration was started.

The unlooked-for discovery of the multitude of plants which flourished upon the earth ages ago, and have been preserved as fossils, led to a further comparison of forms—viz. of those now living with those that have perished. There was no evading the idea that existing species are derived from others now extinct; on the contrary it proved so attractive that it was followed up with the greatest interest and zeal. Then these inquiries into the parentage of species naturally led further to the whole problem of their origin—in short, to a study of the history of species.

The range of vision continued to become yet wider. It is impossible that the dwarf willows and birches found living in Greenland at the present day should be descendants of the maples and beeches which grew there in the Tertiary Period, or that the alders or pines now flourishing on the soil above the beds of bituminous coal at Häring in Tyrol should have sprung from the Proteaceæ and Myrtaceæ which formerly covered the same ground, as we learn from the fossil remains found there. Local changes must have taken place, and the various floras must have undergone a process of expatriation on a large scale not unlike that of men at the time of the migration of tribes. New realms were then occupied by those floras in a manner corresponding to the formation of states by the struggling and mingling races and nations of mankind. The knowledge of the fact that a plant's form depends at the present day upon soil and climate entitles us, moreover, to infer that a similar connection existed in past times between the forms of plants and their



conditions of life, and enables us to discover what gave rise to migrations and caused the redistribution of floras. These phenomena are the subject-matter of the History of the Plant World in the fullest meaning of the phrase; and their explanation is eagerly sought by modern botanists.

In 1853 Unger, to whom all branches of Botany were equally familiar, made the first attempt at such a history of plants. Since then a great number of new discoveries have been made both in the Old World and the New. Men with minds intent upon this object are everywhere searching for the fossil remains which throw such valuable light upon it; but, so far, this—the most recent branch of Botany—has not led to a comprehensive result. We find ourselves, as it were, in the midst of a stream in full flood owing to the number and magnitude of its tributaries, and it is no easy matter to steer clear of shoals and run safely into harbour. Some decades hence it may perhaps be possible to write an accurate and complete history of the plant world founded upon the mass of authentic evidence which will by that time have been winnowed from the records of past ages. At present I must content myself with sketching in general, and often ill-defined, outline the changes which take place in the world of plants.

The foregoing introductory remarks concerning the sources from which materials for a history of plants are derived serve also to explain the arrangement of the subject-matter to be dealt with in the Second Volume of this work. The order of presentation of the different parts of the subject will follow the stages of development of the science. A history of the entire plant-world considered as a single great community must be preceded by a history of species. But each species is the sum of numberless individuals, which are alike in constitution and have the same external characteristics, and a history of species therefore presupposes a knowledge of the history of the individual. Accordingly, our first business is to describe the rejuvenescence, multiplication, and distribution of individuals, and to show by what means a plant, considered as a separate organism, maintains itself, takes possession of its habitat, and is enabled to keep its hold on that habitat up to the moment when it is replaced by descendants endowed with a vitality of their own.

#### THE LANGUAGE OF BOTANISTS.

Before entering upon a description of any of the above phenomena, I feel it necessary to say a few words respecting the technical botanical terms of which I shall make use. The need of short and compendious names to denote particular forms, particular organs, and particular processes, has been always universally recognized, and more or less appropriate additions to our vocabulary have been made by men of science from time to time. As might be expected, these designations are not only an expression of the particular standpoint to which, at the time of their invention, the actual knowledge of plant-life had most recently attained; but they are also liable to bear the stamp of theories advanced by eminent

naturalists of the day, or of the hypotheses which happened to be then in vogue. The progress of true knowledge is too often hindered by the fact that men exalt their speculative theories to the position of "laws of nature", and when they first encounter contradictory evidence twist and turn it until it appears actually to verify those theories. We need not inquire in these instances how much is due to self-deception and how much to prejudice and dogmatism on the part of the investigators. Certain it is that such a perverse method of research, especially when supported by the authorized beliefs of the thoughtless multitude, acts as a drag on true science. Fortunately, however, it is nothing worse than a drag. For, sooner or later, the conviction again asserts itself that our notions respecting the history of plants must be derived from the facts observed in their entirety and purity, instead of facts being made to fit a preconceived opinion—some being explained away as exceptions, whilst others are altogether ignored and suppressed.

In all sciences for which it is requisite to invent technical terms—and in Botany no less than in others—we find that the terminology bears traces of ideas formed at earlier periods, and now rejected as being based on insufficient experiment or imperfect observation, on self-deception or prejudice, as the case may be. The question has, therefore, repeatedly been raised whether it is better to retain such names and modes of expression, although they are likely to suggest wrong ideas to students, or to abolish them and substitute new ones in their stead. There are strong arguments for both courses. The chief advantage of retaining the old terms is that readers of modern works are thereby enabled to understand more easily the writings of older botanists. We have also to consider the probability that in rejecting old terms and inventing new ones we may fall into the same errors as our predecessors. Any one who has worked in the field of Botany for more than forty years, as I have done, must have found that on an average every ten years prevailing ideas have undergone a change. He has seen how theories, which for a time influenced every branch of the science, and were actually standard conceptions in many departments of research, have sooner or later had to give place to new ones. He knows how often a naturalist is compelled, in consequence of fresh and unexpected discoveries, to let go a position which he has considered impregnable, and which has become endeared to him by long familiarity. Thus, experience teaches diffidence, and one learns to attribute only a temporary value, so to speak, even to one's own original theories, and to rest assured that, in a few decades, what now appears to be nearest the truth will be superseded by something else which comes still nearer to it.

But if, whenever a fresh stage of knowledge were reached, all terms and phrases which had become antiquated and no longer quite applicable were abandoned and replaced by others, and if in addition new names were introduced corresponding to every modification in the results obtained by observing all the different processes and appearances with which we have to deal, our science would inevitably be rendered far less accessible—and this consequence would be much to



be regretted. However strong the desire to understand the secrets of plant-life, it could only be satisfied at the cost of learning a special scientific language; and Botany would become, in an even greater degree than is the case at present, a close study for specialists, instead of being the common property of the many inquiring minds to whom the results of our researches by right belong.

Accordingly, we shall retain so far as is practicable the recognized scientific terms. Where they are no longer quite suitable they will be briefly elucidated; and, when the conceptions to which they refer have been expanded or limited, the old established names will also be taken in a wider or a narrower sense as the case may be. New expressions will only be introduced where their use is productive of greater clearness and distinctness in the ideas involved; and even these additions must be in harmony with the terms already in existence.

It is worthy of note too that many foreign words, which have been longest established and also subject to frequent use by botanists, originally meant something altogether different from what they are intended to denote at the present day. In the very first section of this volume a whole series of such words will be employed. The history of the plant-individual is there dealt with. What is an "individual"? The word comes from *dividere*, to divide, and denoted originally a thing which is not divisible. But there is no such thing as an indivisible plant. The survival of plants, their reproduction and multiplication, are all dependent on processes of division; and any species whose individuals were not divisible, would be doomed to inevitable destruction. The characteristic property of an individual cannot therefore lie in absolute indivisibility. A qualification has in consequence been inserted in the definition, and an individual is explained to be a thing which cannot be divided without ceasing to be, as heretofore, an organized being subsisting independently, in which each single part belong indispensably to the whole. Even this definition is not appropriate to a plant. The living protoplast of a unicellular plant—an organism which must without question be conceived as an individual—divides into two halves, which separate from one another and constitute two independent individuals. This instance affords, however, an indication of the true definition. A plant-individual is an organism which can and does live independently and without the aid of other organisms of the same form. There are plant-individuals each of which consists of a single protoplast, whilst others are composed of many protoplasts living together. In the latter there is for the most part a division of labour accompanied by a corresponding variety in the forms of the different parts of the individual; but even in these cases individuality is not necessarily destroyed by division. Where division of labour has been carried so far as it is in a plant provided with stem and leaves (*cf.* vol. i. p. 584), it used to be thought necessary to look upon the structure as an association of individuals. Each single shoot was conceived to be an individual because it possessed the power of continuing to live after it had been separated from the axis, and on that assumption each one of the higher plants was built up of such and such a number of separate individuals. Later on, however, inasmuch as every branch of a shoot

is capable of living when separated from the rest and of producing a new independent plant, the parts of a shoot came to be considered as being individuals, and the term "Anaphytes" was applied to them. We shall see hereafter the extent to which this conception is of importance in relation to the subject of alternation of generations. It would be out of place to treat it more fully at present.

Another conception of the plant-individual must also be mentioned here. When the impossibility of defining it as indivisible was recognized, the strange expedient was invented of assuming the existence of divisible individuals and of representing all parts which have been produced asexually and have become independent as belonging to a single individual. A potato puts forth thirty or forty fresh tubers in the course of a few years, and all these were considered as collectively constituting one single individual, as also were the countless young carnation-plants which are to be derived by means of cuttings from one old plant. The general rule was that only an organism produced by sexual process was to pass as an individual. Cuttings, tubers, and the like, detached from such an organism would be, according to this conception, merely parts of one individual, even though they were capable of living quite independently and at a distance from one another.

This definition, the invention of philosophers, has never been taken seriously by naturalists, and I only cite it because it introduces another important problem which I purpose to treat in an exhaustive manner in the first three sections of this volume, namely, the question of the propagation or generation of plants. The modes of reproduction in plants have been subjected in recent times to most patient investigation on the part of botanists gifted with the keenest powers of observation, and their researches have led to the conclusion that in most—probably in all—divisions of the vegetable kingdom two kinds of propagation occur. In each case a single protoplast forms the starting-point for the new individual; but, in the one, this protoplast does not require the special stimulus afforded by union with another protoplast, whereas, in the other, in order that a new individual organism may be produced, a pairing—*i.e.* a union of the substances—of two protoplasts, which have come into being at different spots, must take place. The former is called *asexual* reproduction, the latter *sexual* reproduction. All reproductive bodies arising asexually are included under the name of *brood-bodies*, whilst those which are associated with the sexual process may be termed broadly *fruits*.

There are all grades of brood-bodies, from the single cell to the completely formed plant. Brood-bodies, if unicellular, are termed *spores*, if multicellular, *thallidia*; and those which constitute rudimentary shoots are called *buds*. The bud form of brood-body either detaches itself from the living parent-plant, or else, as more frequently happens, it becomes independent through the death of the plant from which it sprang. In the latter case the off-shoots remain in the immediate vicinity of the parent-plant. In the case of trees and shrubs the buds do not sever themselves from the axis on which they were developed, but continue their connection with it as they grow into shoots, and in this manner are formed those compound individuals to which reference has been already made. It is much less

common for full-grown shoots to detach themselves from the parent-plant and act as brood-bodies.

Fruits of all degrees of complexity are also found. They are sometimes single cells, sometimes groups of cells, and sometimes complete plants in miniature. Usually the fruit—or at least the most important part of it which contains the fertilized ovum or the embryo produced thereby—becomes detached, when ripe, from the parent-plant; but, in many groups of the vegetable kingdom, in Ferns, Mosses, Lichens, and Floridæ, for example, the fruit remains at its place of origin and preserves its connection with the mother-plant whilst itself developing into a new generation, which, however, does not produce fruits but spores. When asexual and sexual reproduction take place alternately in a definite manner, we speak of an *Alternation of Generations*. Hitherto the subjects of fruit-formation and of the alternation of generations in their relation to the History of Plants have remained unrecognized and unelucidated. In one of the following sections of this volume an attempt will be made to solve this great mystery.

# THE GENESIS OF PLANT-OFFSPRING.

---

## 1. ASEXUAL REPRODUCTION.

Spores and Thallidia.—Buds on Roots.—Buds on Stems.—Buds on Leaves.

### SPORES AND THALLIDIA.

In the chapters on ferns in the old herbals, attention is invariably directed to the extraordinary phenomenon that the plants in question do not produce flowers or fruit, and yet propagate their kind and multiply abundantly, and the remark is made that these plants will often spring up quite unexpectedly in caves, or in the cracks of old walls, without any seeds having been previously perceptible there. Hence in Germany a fabulous story was invented that the seeds of ferns were formed in a mysterious manner at the time of the summer solstice only, and that these seeds could only be collected on Midsummer Eve by persons initiated in the mystery who made use of certain magic words on the occasion. Hieronymus Bock or Tragus, as he called himself in accordance with the then prevailing fashion of translating names into Greek, preacher and physician at Hornbach in 1532, was the first to contradict this childish superstition, and to convince himself of the possibility of obtaining "fern-seeds" without the use of incantations. In his Herbal, published in 1539, he gives the following account, which is in many respects interesting, of his endeavours to collect the seeds of ferns: "All our teachers write that the fern bears neither flower nor seed; nevertheless, I have four times looked for the seed in the night of Midsummer Eve, and have found early in the morning before daybreak small black seeds like poppy-seeds on cloths and on the broad leaves of mullein beneath the stems in varying quantities. . . . I have used no charm or spell in this matter, but have looked for the seeds without any superstition and have found them. One year, however, I found more than another, and I have sometimes been out without success. I have not gone alone to fetch the seeds, but have taken two others with me, and have made a great fire in an unfrequented spot and let it burn all through the night. How the thing came to pass, and what secret nature intends to reveal by it, I cannot tell. I have stated all this because all our teachers describe the fern as being without seeds."

There can be no doubt that by the brown seeds Hieronymus Bock meant those structures which, about two centuries later, were named "spores" by Linnæus. But even in the time of Linnæus the whole subject of spores, especially in their relation to fruit, was shrouded in complete obscurity. The word "spore" is derived from



the Greek, and signifies etymologically precisely the same as "seed", and spores were considered to be peculiar seeds, formed by means of some mysterious processes of fructification. As late as fifty years ago the spore was defined as "that part of a cryptogamic plant which corresponds to the seed, and from which, although it contains no germ, a new plant can be developed".

The mode of fructification in the Fern, and, in general, the entire history of its development, were discovered for the first time in 1848. It was then shown that these plants pass through two kinds of regularly alternating generations. One of these is itself inconspicuous, but bears reproductive organs and produces fruits; the other, springing from the fruit, which continues its connection with the parent-plant, is distinguished by fronds and produces spores. Thus the fronds of Ferns bear no sexual reproductive organs, and the spores formed upon them cannot therefore be looked upon as fruits or even as seeds, a seed being part of a fruit.

Some people, it is true, treat the entire frond-bearing Fern-plant as a fruit and the spores on the fronds as part of this fruit, although such a theory involves the admission that fruits may strike root, multiply by means of runners and continue to grow for many years, putting forth annually new spore-bearing fronds. According to this view, which I cannot endorse, a gigantic tree-fern, aged a hundred years, would be a fruit, and to be consistent it would be necessary to regard a whole grove of Horse-tails as belonging to one single fruit. Other botanists, whilst denying that the Fern-plant with its roots and fronds is the fruit itself, are yet of opinion that the formation of spores in the Fern is a consequence of the process of fruiting, inasmuch as the Fern-plant would never make its appearance at all but for the formation of fruit by the previous generation; and they hold that the spores of Ferns, and of their allies the Horse-tails and Club-mosses, should on that account be distinguished from those of other Cryptogams. To this view there are two objections. In the first place, we know many cases wherein a Fern-plant with spore-bearing fronds is developed from the first generation without any formation of fruit having taken place, and the plant in these instances is in no way different from those which have sprung from fruits of the first generation. Secondly, it is difficult to see why the sporogenous generation should be more dependent on the fruit of the first generation in the case of Ferns than in many other Cryptogams, which similarly exhibit an alternation of generations.

As the spores of Ferns, and of Cryptogams in general, are not the direct result of a process of fertilization, they are not parts of fruit, but are brood-bodies. They should be placed by the side of the bud forms of brood-body presently to be described, though differing from these in that they always produce a single layer (*i.e.* a thallus) only, and never a leafy, axial structure. They are just as characteristic of Cryptogams as buds are of Phanerogams or Flowering Plants, and as the name of Cryptogam is no longer quite appropriate, it is often replaced by the term "sporogenous plant". Before the discovery of the alternation of generations in Cryptogams, the name spore was applied to many fruits and rudiments of fruits, particularly where these happened to be unicellular, an error which we should be

careful to avoid at the present day. When we come to the description of fruits and their origin, we shall have occasion to return again to this subject.

The places where spores originate are remarkably varied. In some plants nests of cells make their appearance in the interior of an extensive tissue; in others single cells are exposed on the surface. The task of spore-development devolves sometimes upon a part of a green stem or leaflet. Sometimes—in plants devoid of chlorophyll—upon the protoplasmic contents of a tubular structure, and sometimes upon the abstricted ends of hyphal filaments. The best way to arrive at an idea of the extreme diversity in this respect is to classify spores in groups according to their mode of origin.

One group comprises all such spores as are formed in the cells of a tissue. Amongst these are the spores of Ferns, Rhizocarps, Horse-tails, Club-mosses, and the numerous kinds of Mosses and Liverworts. In one sub-group of Ferns papillæ spring singly from the epidermis clothing the ribs of the fronds, each papilla being divided by a transverse wall into a free extremity and a stalk-cell. Both cells of the papilla become partitioned so as to form bodies of tissue, and the one that develops from the free terminal cell assumes an oval or spherical shape. In this latter ball of tissue a tetrahedral central cell and an envelope composed of several layers of cells may be distinguished. By internal partition of the central cell a little cluster of cells is formed, whilst, in the meantime, the inner layer of cells composing the envelope is dissolved, so that the whole now assumes the aspect of a receptacle inclosing a ball of cells embedded in a fluid matrix. Each cell of the cluster next divides into four compartments, and the protoplasts which constitute the contents of these chambers provide themselves with membranes and become disconnected upon the solution of the framework of their home. These separated cells are the spores. To the naked eye they have the appearance of a powdery mass. As has been said, of the cell-layers which formed the envelope of the sporogenous tissue, only the inner one was dissolved; the outer layer persists and constitutes a kind of capsule, to which the name of spore-case or "sporangium" is applied (see figs. 189<sup>13</sup>, 189<sup>14</sup>, 189<sup>15</sup>). A collection of sporangia of this sort is called a "sorus". In the Polypodiaceæ—a family of Ferns to which the majority of European species belong—the sori may be seen on the backs of the fronds (see 189<sup>5</sup>). Upon the veins running through the green tissue are seated little cushion-like groups of cells. Each cell in one of these cushions is capable of developing into a stalked sporangium, and sometimes a single sorus consists of no less than fifty such stalked sporangia. In the Cyatheaceæ also, which include most of the Tree-ferns, the sori are developed on the under side of the fronds, but in their case each is borne on a kind of peg projecting at right angles to the surface of the frond. The sporangia derived from the epidermal cells of this peg are very shortly stalked. An annular wall is produced from the green tissue of the frond and surrounds the sporangiferous peg, which consequently stands up from the middle of a cup (see figs. 189<sup>10</sup>, 189<sup>11</sup>, 189<sup>12</sup>).

In the delicate and graceful Hymenophyllaceæ—Ferns with a resemblance to





Fig. 189.—Ferns.

*Nephrolepis Duffi*. <sup>2</sup> *Trichomanes Lyelli*. <sup>3</sup> Sorns of the same Fern with cup-shaped investment seen in longitudinal section. <sup>4</sup> *Rhipidopteris peltata*. <sup>5</sup> *Polypodium serpens*. <sup>6</sup> Pinna of *Gleichenia alpina*. <sup>7</sup> *Schizaea fistulosa*. <sup>8</sup> *Botrychium lanceolatum*. <sup>9</sup> Under side of a pinna of *Gleichenia alpina*; in the two upper cavities the sporangia are covered by leaflets, in the under ones they are exposed. <sup>10</sup>, <sup>11</sup> Pinna of *Cyathea elegans*. <sup>12</sup> Longitudinal section through a Sorus and Cup of *Cyathea*. <sup>13</sup> Sporangium of *Cyathea*. <sup>14</sup> Sporangium of *Polypodium*. <sup>15</sup> Sporangium of *Schizaea*. <sup>16</sup> Under side of the Prothallium of Spleenwort. 1, 2, 4, 5, 6, 7, 8 natural size; 3, 9, 10, 11, 12, 13, 14, 15, 16 magnified from 5 to 20 times.

Mosses, and belonging for the most part to tropical regions—the veins of the pinnæ project beyond the margin of the green tissue and form styloid processes whose epidermal cells become the points of origin of sporangia. Each styloid process thus constitutes an axis bearing the sporangia, and the entire sorus has the form of a little spike. But the sorus itself stands in a cup formed by an upgrowth of the green tissue at the margin of the pinna (see figs. 189<sup>2</sup> and 189<sup>3</sup>).

In the three groups of Ferns above dealt with the sporangia arise from epidermal cells. In the Gleicheniaceæ and Schizæaceæ (two specimens of which are shown in figs. 189<sup>6</sup> and 189<sup>7</sup>) the sporangia are modified leaflets. We must here remark that the fronds of Ferns in spite of their similarity to foliage-leaves are not to be regarded as such, but as phylloclades, whilst the scales upon the fronds must be considered to be leaves. We shall refer to this again later on. Now, in Gleicheniaceæ and Schizæaceæ some of these small scaly leaves are metamorphosed into sporangia which here take the form of rounded bodies set in rows of pit-like cavities hollowed out of the pinnæ, whilst other scales constitute protective coverings to these sporangia. The relation existing between the various parts in the case of a pinna of *Gleichenia alpina* is shown very clearly on an enlarged scale in fig. 189<sup>9</sup>.

In respect of origin and development the spores and sporangia are again quite different in the group of Ferns comprised under the name of Ophioglosseæ, one species of which—viz. the spear-shaped Moonwort (*Botrychium lanceolatum*)—is represented in fig. 189<sup>8</sup>. In these Ferns, the sporogenous portions take the form of nests of cells embedded in the tissue of the frond. The cells in these niduses become partitioned each into four chambers, and the latter contain protoplasts, which surround themselves with membranes and become spores. The spores are set at liberty as a consequence of the solution of the walls of the chambers, and they occupy, in the form of a fine powder, little vesicular cavities in the tissue of the pinnules. The epidermis of these pinnules now serves as the wall of the cavities, i.e. of the sporangia.

Each plant in the group of the Ophioglosseæ exhibits two kinds of frond: the one kind develops no spores and has the appearance of a green foliage-leaf; the other produces sporangia, which are arranged either like bunches of grapes or in spikes consisting almost entirely of the sporangia (see fig. 189<sup>8</sup>). A similar arrangement may be observed also in many Ferns belonging to other divisions, as, for instance, in the genera *Allosorus*, *Struthiopteris*, and *Blechnum*, representatives of which occur in the European Flora as well as in others. In other cases, such as the Flowering Fern (*Osmunda regalis*), for example, sporangia are only formed on the upper portion of a frond, whilst the lower segments are foliaceous. A very peculiar form is that of *Rhipidopteris peltata*, a fern indigenous in the mountainous regions of Mexico (see fig. 189<sup>4</sup>). Besides the flat, fan-shaped fronds which produce no sporangia, other fronds shaped like funnels or shallow bowls are developed, and the spore-cases are produced from the epidermal cells in the hollows of these fronds.

In the last case it is worthy of note that the sporangia are formed on the upper



surface of the frond, for this is of very uncommon occurrence. They are usually situated on the under surface of the frond, the reason being that they are thus best sheltered from both rain and sun. Most instances exhibit in addition a further safeguard against excessive moisture or desiccation in the form of a special awning covering the sporangia. This awning is either an outgrowth from the cells forming the apex of the sporangiferous cushion or peg, and takes the form of a delicate membrane stretched over the whole sorus and known as an *indusium*, as in our male Shield Fern (*Aspidium Filix-mas*), or else small, scale-like leaflets spread themselves over the sporangia, as in the *Gleichenias* (fig. 189<sup>9</sup>), to which reference has already been made, and in the no less remarkable *Lygodiums* and *Davallias*. Sometimes five or six squamous leaflets stand in a circle round the sporangia and envelope them so that the whole looks deceptively like a closed flower, as in the genera *Schizocæna*, *Hymenocystis*, and *Diacalpe*; or, these leaflets form a sort of box, which opens with a lid, as in *Cibotium*. In other cases, again, membranous bands or borders grow up from the surface of the frond, and the sporangia, which are arranged in a long line, are covered over by them, as occurs in *Lindsaya* and *Blechnum*; or, the margin of the frond is split and the sporangia are hidden in the narrow cleft thus made, as in *Vittaria* and *Schizoloma*. Often the margin of the frond is folded over, thus covering the sporangia, which are here developed on raised cushions; *Allosorus*, *Ceratopteris*, *Ceratodactylis*, *Parkeria*, and many other genera exhibit this formation. The extreme variety prevailing in this class of adaptation is connected with differences in the climatic conditions of the habitats where the plants in question live. Any attempt to deal with individual contrivances here would lead us too far.

The Rhizocarpeæ are a group nearly allied to Ferns, and they naturally follow the same lines as Ferns in the formation of their spores and sporangia. *Salvinia* reminds one to some extent of the Hymenophyllaceæ, at any rate as regards the outgrowth of an annular wall below the sporangia (the latter being in this case also borne on a fusiform axis), and also as regards the development of this wall, which becomes closed at the top into a complete box enshrouding the sporangia. *Marsilea*, on the other hand, exhibits stalked, bean-shaped capsules with cavities in which the sporangia are formed on raised cushions.

The Club-mosses (*Lycopodiaceæ*) also bear a striking resemblance in their mode of spore-formation to Ferns, especially to the various species of *Lygodium* and *Lygodictyon*, genera of which mention has already been made. The first rudiments of the sporangia are swellings at the base of the little squamiform leaves, or on the axis just at their insertion. The internal tissue of this protuberance is marked off in the form of a roundish ball. The cells constituting the ball separate and then become segmented each into four chambers, the walls of which are subsequently dissolved. The protoplasts within the chambers inclose themselves in membranes and become free spores. The epidermis originally clothing the swelling persists, and now forms the wall of a bean-shaped sporangium containing loose spores. The sporangium subsequently opens by means of a lid like a box.

Horse-tails exhibit a process of spore-formation quite peculiar to themselves. Two species of this group—namely, *Equisetum arvense* and *E. sylvaticum* are shown in figs. 190<sup>2</sup> and 190<sup>7</sup>. At the top of the hollow stem there is a spike of peltate scales borne on short stalks and arranged in whorls, each of which must, in consideration of its origin, be looked upon as a metamorphosed leaf (*cf.* fig. 190<sup>3</sup>).



Fig. 190.—Horse-tails.

<sup>1</sup> Summer Shoot of *Equisetum arvense*. <sup>2</sup> Vernal fertile Shoot of *Equisetum arvense*. <sup>3</sup> Spike of whorled sporangiophores from the same *Equisetum*. <sup>4</sup> A single sporangiophore. <sup>5</sup>, <sup>6</sup> Spores. <sup>7</sup> *Equisetum sylvaticum*. <sup>8</sup> Prothallium of a Horse-tail. <sup>1</sup>, <sup>2</sup>, <sup>7</sup> natural size; <sup>3</sup>  $\times 3$ ; <sup>4</sup>  $\times 6$ ; <sup>5</sup>, <sup>6</sup>  $\times 25$ ; <sup>8</sup>  $\times 30$ .

On the inner surfaces of the scales—*i.e.* those turned towards the axis of the spike—little warts arise, which develop into sporangia (*cf.* fig. 190<sup>4</sup>). The outer cell-layers of these multicellular warts become the walls of the sporangia, whilst the inner tissue breaks up into cells. These cells then divide into four cells, each of which becomes a spore.



The last division of plants wherein the spores are formed deep down in a tissue is that of the Muscineæ, which include Mosses and Liverworts. In these plants the spore-producing generation consists of a cellular body, which has arisen from the fruit, is usually seated on a stalk, and in shape is cylindrical, pyriform, or more or less spherical (*cf.* figs. 191<sup>3, 4, 7, 8, 15</sup>). We must here remark, by the way, that botanists used formerly to look upon this sporogenous generation of the Moss erroneously



Fig. 191.—Mosses.

<sup>1</sup> *Polytrichum commune*, the sporogonium to the left concealed by the cap, the sporogonium to the right exposed. <sup>2</sup> The same Moss in an earlier stage of development. <sup>3</sup> Sporogonium of *Polytrichum commune* with its lid. <sup>4</sup> The same after the lid has fallen off. <sup>5</sup> *Bryum caespiticium*. <sup>6</sup> Sporogonium of the same Moss with its cap. <sup>7</sup> The same without the cap, but with the lid still on. <sup>8</sup> The same after removal of the lid, showing the teeth (peristome). <sup>9</sup> A piece of the peristome. <sup>10</sup> Antheridia, Archegonia, and Paraphyses of *Bryum caespiticium*. <sup>11</sup> *Hylocomium splendens*. <sup>12</sup> Sporogonium of *Hylocomium splendens*. <sup>13</sup> *Andrea rupestris* with burst sporogonium. <sup>14</sup> *Sphagnum cymbifolium*, its spherical sporogonia still covered by their lids in the left-hand specimen. <sup>15</sup> A single sporogonium of the same Moss. 1, 2, 5, 11, 14 natural size; 3, 4, 6, 7, 8, 12, 13, 15  $\times 5$ ; 9, 10  $\times 150$ .

as the fruit itself. The only structure rightly to be considered as the Moss-fruit is that in which the embryo is produced as a result of fertilization. If afterwards a new generation springs up from the embryo which has been formed in the interior of the fruit, this generation cannot any longer be described as a fruit even in cases

where it remains permanently connected with the mother-plant, as happens in Mosses.

The cells composing the tissues of the cylindrical, pyriform, or spherical body above referred to develop in a variety of ways. Those situated near the outer surface form the wall of a receptacle, and those in the interior, which serve as a filling to the receptacle, form the spores. The process of spore-formation is here much the same as in Ferns. The cells of the central mass, at first united into a tissue, in time become isolated; each divides into four, and the spores are ultimately developed from these protoplasts. The spores are then left free in the form of a fine powder within the receptacle, which is called a sporogonium. In most Liverworts, a group nearly allied to the Mosses, certain other cells having a curious structure are formed from the internal tissue besides the spores. These are the so-called "elaters", and they serve to scatter the spores. In a few Mosses a sort of central column remains in the middle of the sporogonium in addition to the spores when the whole is mature. Externally the sporogonia of Mosses differ very little from the cellular bodies out of which they were developed; like them, they are spherical, pear-shaped, or cylindrical as the case may be. But the part which subsequently opens and liberates the spores at the proper time exhibits in its more minute anatomy considerable differentiation. This subject and that of the elaters mentioned above will be again referred to in the section devoted to the distribution of spores.

As with the sporangia in Ferns, so also in Mosses the sporogonia are protected during development from injurious external influences, especially desiccation, and are wrapped in coverings which vary considerably according to their origin. In Mosses a kind of cap is usually to be seen covering the young and tender sporogonium (see fig. 191<sup>1</sup>), and this structure has its origin in the fruit from which the sporogenous generation (or *sporophyte*) has sprung, the coat of the fruit being torn away and its upper part carried up in the form of a cap by the sporophyte during its growth from the embryo. Later on, when the sporogonium is no longer in need of protection, and the presence of a cover would be detrimental in that it might prevent the spores from being scattered, the cap is cast off.

All the spores hitherto discussed originate within a tissue, and their history involves the conversion of the protoplasmic contents of each compartment of the reproductive part of the tissue into a spore. A second group of spores is composed of those which arise from the breaking up of the protoplasmic contents of tubular, club-shaped, or spherical cells not united in tissues, and are set free from their birthplaces as soon as they are formed. The cells thus constituting the mother-cells of spores may, by analogy, be conveniently termed sporangia. The process of formation of spores within them appears to be much simpler than in Ferns, Club-mosses, Horse-tails, Mosses, and Liverworts. Speaking generally, the only striking differences occurring in these cases are such as affect the number and shape of the spores which escape from a sporangium.

As described in the first volume of this work (*cf.* vol. i. p. 23, and Plate I. *a-d*),

the filamentous organism *Vaucheria* produces a single comparatively large green spore in each of the club-shaped outgrowths developed by the tubular branches of the plant, and each spore thus formed is able, when free, to swim about by means of its numerous short cilia. On the other hand, the mould-like Saprolegniaceæ, which live under water upon decaying animals, develop a large number of colourless spores in their clavate filaments, and these after escaping from the tubes whirl about in the water by means of two long revolving cilia (*cf.* fig. 192). In both



Fig. 192.—Swarm-spores of Saprolegniaceæ and Chytridiaceæ.

<sup>1</sup> *Achlya prolifera*. <sup>2, 3, 4</sup> Development and escape of swarm-spores of *Achlya prolifera*. <sup>5</sup> *Chytridium Ola* parasitic upon the oogonium of *Edogonium*; development and escape of swarm-spores. <sup>6</sup> *Saprolegnia lactea*. <sup>7</sup> Development and escape of the swarm-spores of *Saprolegnia lactea* (partly after De Bary and Pringsheim). <sup>1</sup>  $\times 20$ ; <sup>2, 3, 4</sup>  $\times 400$ ; <sup>5</sup>  $\times 300$ ; <sup>6</sup>  $\times 100$ ; <sup>7</sup>  $\times 300$ .

these instances the spores themselves possess the power of movement and of swarming about in water, whence they are called "swarm-spores". The name "zoo-spores" ( $\xi\omega\nu$  = animal) has also been applied to them on account of their decided resemblance in form and behaviour to certain Infusoria.

The delicate, profusely-branched mycelia of the Moulds, included under the name Mucorini, give rise to special filaments which grow straight upwards. These erect hyphæ divide into two cells. The upper cell becomes a spherical bladder, and the under a long slender stalk, the upper end of which protrudes in the form of a hollow stopper into the bladder supported by it (*cf.* fig. 193<sup>2</sup>). The protoplasm in the upper, vesicular cell breaks up into a large number of spores and thus



becomes a sporangium. The increase in weight of the sporangium causes the filiform stalk to bend; the sporangium bursts, and the spores, together with the clear fluid in which they are suspended, issue through the rent in the sporangium (*cf.* fig. 193<sup>1</sup>).

In the Moulds of the family of the Mucorini the sporangia are for the most part



Fig. 193.—Moulds.

- <sup>1</sup> *Mucor Mucedo*;  $\times 40$ . <sup>2</sup> Longitudinal section of a sporangium of *Mucor Mucedo*;  $\times 260$ . <sup>3</sup> Fruit-formation in *Mucor Mucedo*;  $\times 180$ . <sup>4</sup> *Aspergillus niger*;  $\times 30$ . <sup>5</sup> Longitudinal section of a sporophore of *Aspergillus niger*. <sup>6</sup> Fructification of *Penicillium crustaceum* (after Brefeld). <sup>7</sup> Fruit-formation in *Aspergillus* (after Eidam). <sup>8</sup> *Penicillium crustaceum*;  $\times 40$ . <sup>9</sup> Sporophore of *Penicillium crustaceum*;  $\times 200$ .

closely crowded together, but they are never walled in by a tissue or surrounded by any particular envelope. They are, moreover, always separate, and have the appearance of a miniature plantation. A different state of affairs is found in that group of Fungi known as the Ascomycetes, a group which includes, amongst well-

known plants, the genera *Morchella* and *Helvella* (cf. fig. 194), Lichens, and also several mould-like forms, notably the Erysipheæ, which produce Mildew, and *Claviceps*, which is the cause of Ergot of Rye. In these plants the ends of the hyphæ stand up from restricted areas of the mycelium, some in the form of long clavate tubes, some as delicate filiform paraphyses, the group of tubes and paraphyses being surrounded by other cellular structures in such a manner that the whole has the appearance of a dish or cup or capsule. The protoplasm in the tubes breaks up and forms either ellipsoidal bodies arranged usually in linear series (cf. fig. 194<sup>2</sup>) or long fascicled threads, which, whilst still inclosed in the

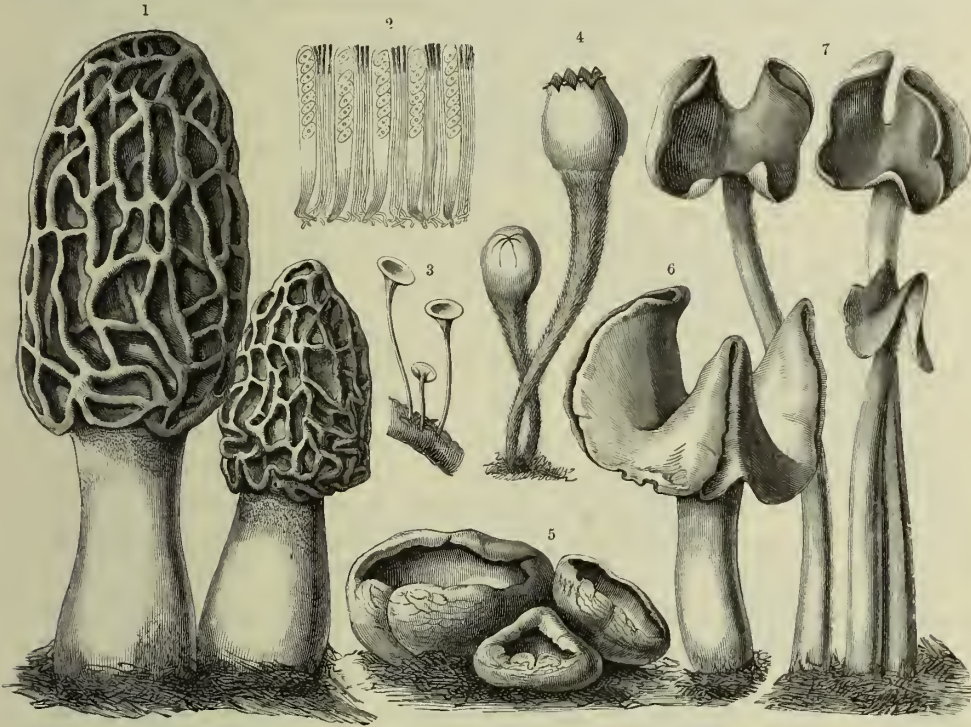


Fig. 194.—Discomycetes.

<sup>1</sup> The Morel (*Morchella esculenta*). <sup>2</sup> Longitudinal section from the hymenium of *Morchella esculenta* showing five filaments each containing eight spores and filiform paraphyses in between them. <sup>3</sup> *Helotium Tuba*. <sup>4</sup> *Anthopeziza Winteri*. <sup>5</sup> *Peziza vesiculosa*. <sup>6</sup> *Helvella Infula*. <sup>7</sup> *Helvella fistulosa*. <sup>1</sup>, <sup>4</sup>, <sup>5</sup>, <sup>6</sup>, <sup>7</sup> natural size; <sup>3</sup>  $\times 4$ ; <sup>2</sup>  $\times 120$ .

tubes, put on a stout cell-wall. The name of *asci* (ἀσκός = a leather bag) has been given to these sporangia, and *ascospores* to the spores which they contain. They are destitute of cilia, the distinguishing mark of zoospores, and have no power of independent motion after their extrusion from the tubes, which takes place through a rent at the top.

There is great variety in the mode of grouping, as also in the envelopment of the sporogenous tubes in different genera and species. When the tubes grow from the bottom of flask-shaped excavations or pits, the whole structure is spoken of as a *perithecium*; if they stand in a shallow patelliform cavity or on the surface the



term used is *apothecium*. Perithecia and apothecia have been erroneously called fruits also. The same principles must here be applied as governed our consideration of Ferns and Mosses. Even if the genesis of perithecia and apothecia is really preceded by a process of fertilization, still the only part properly to be called a fruit is the tissue in which one or more protoplasts have become embryos in consequence of the act of fertilization. • The outgrowth from this fruit is precisely the new generation; and it does not matter at all whether this new sporogenous generation preserves its connection with the previous fruit-forming generation or not. Perithecia and apothecia, and, in general, all so-called fruits in the Ascomycetes are therefore equivalent to the sporogonia in Muscineæ and to the sporangiferous plants in Horse-tails, Club-mosses, and Ferns.

We shall place together in a third group all spores which arise neither singly in the cell-compartments of a tissue nor through the breaking up of the protoplasm within a tube, but by abstriction and abjunction. The process of spore-formation in these cases is as follows:—The protoplasm, which is inclosed in a cell-wall, produces an internal partition whereby it is itself divided into two halves, and the cell-cavity into two chambers. As soon as this has taken place the partition-wall splits and the two cells fall asunder. If the cell which undergoes the process of bipartition is in the form of a blind tube or sac, and if the partition is intercalated near the tip of the sac, the effect produced is as though the end of the sac had been tied off or abstricted and had then dropped. The part remaining behind now constitutes another blind sac, and in some genera the process of abjunction from the extremity may be repeated over and over again. *Basidium* is the name given to a closed sac of this kind from which spores are abstricted, it forming in a manner a base for the spores. This term has hitherto only been employed by botanists in relation to the so-called Basidiomycetes (which includes the Fungi known as Mushrooms and Toadstools), but it is justifiable to extend its application to all other structures which play the same part.

Abstriction of spores is exhibited at its simplest in the plant known as the Rust of Wheat, which at a certain stage of its development lives as a parasite in the green tissue of the leaves of our species of Wheat. For the purpose of spore-formation tufts of hyphæ project beyond the surface of the infested leaves. At the extremity of each hypha, which is in the form of a closed sac, a single spore of comparatively large size is developed; and after the fall of this one spore the hypha or basidium has lost the power of abstricting others.

A similar phenomenon is observed in the Fungi belonging to the genera *Hydnum*, *Polyporus*, *Agaricus*, and *Clavaria*, of which several examples are represented in fig. 195. Their basidia are club-shaped, and terminate in four slender filaments, the so-called *sterigmata*, and from the end of each sterigma one spore is abjointed (fig. 195<sup>7</sup>). These basidia, together with a number of slender sac-like tubes, to which reference will again be made when the Basidiomycetes are described in detail, beset certain structures projecting from the under surface of the cap-shaped sporophore—these structures being lamellæ or spikes or tubes



as the case may be. *Aspergillus niger* (see fig. 193<sup>4</sup> and 193<sup>5</sup>), a Mould living chiefly on the juices of fresh or preserved fruits, develops slender upright hyphæ with swollen ends, which bear numbers of short peg-like processes—the sterigmata—from which moniliform series of from five to eight spores are abjoined in



Fig. 195.—Basidiomycetes.

<sup>1</sup> *Clavaria aurea*. <sup>2</sup> *Dædalea quercina*. <sup>3</sup> *Marasmius tenerrimus*. <sup>4</sup> *Marasmius perforans*. <sup>5</sup> *Craterellus clavatus*. <sup>6</sup> *Amanita phalloides*. <sup>7</sup> Clavate basidia with filamentous sterigmata, from the ends of which spherical spores are abjoined (from the hymenium of *Amanita phalloides*). <sup>8</sup> *Hydnum imbricatum*. <sup>9</sup> *Polyporus perennis*. 1, 2, 3, 4, 5, 6, 8, 9 natural size; 7  $\times 250$ .

rapid succession. These spores at first hang loosely together, and are arranged like strings of pearls, but collectively these rows of spores form a spherical head. A shock of any kind, especially the disturbance occasioned by currents of air, will cause a severance of the spores, and the entire sphere consequently falls to pieces.

Nothing then remains but the hyphal filament with its swollen end beset with pegs and looking like a club armed with spikes (*cf.* fig. 193<sup>4</sup>).

Also in *Penicillium*, the commonest of all Moulds, the spores are abjointed from the sterigmata in moniliform rows; but in this case the erect hypha which bears the spores is septate and not clavate at the extremity, and terminates in forked branches, so that the chains of spores are grouped like the hairs in a camel's-hair pencil. A species of *Penicillium*—viz. *P. crustaceum*—is represented in fig. 193<sup>8</sup> and 193<sup>9</sup>). In the Peronosporæ, to which class belongs the parasite *Cystopus candidus*, celebrated for its fatal effects on cruciferous plants, moniliform rows of spores are abjointed from the basidia without the intervention of sterigmata. The mode of arrangement of the chains of spores in this parasite is, however, not quite like that in either *Penicillium* or *Aspergillus*.

A further diversity in this kind of spore-formation by process of abjunction is introduced by the presence in several families of plants of special envelopes surrounding the abjointed spores. Particular cases of this are afforded by Gasteromycetes (Puff-ball family) and Florideæ (Red Seaweeds) and by that stage in the development of the Rust-Fungus which is known by the name of *Æcidium*. The æcidia make their appearance in the form of structures growing out from a mycelium infesting the green tissues of leaves. The basidia are formed by the ends of hyphæ which stand up in dense crowds. Moniliform chains of spores are abjointed from the basidia and are enveloped by a sporangium-like wall developed from the cells surrounding the basidia. It is not till this enveloping capsule bursts that the spores are set free and can be distributed.

In the large Puff-Ball family (Gasteromycetes) the same process takes place, but the basidia and spores are not arranged so regularly, and amongst the spores are to be found other hair-like, cellular structures which constitute what is termed a *capillitium* and are of especial importance in relation to the distribution of the spores. Florideæ develop their spores within receptacles peculiar to themselves, which frequently resemble urns or capsules, and might be designated sporangia for the sake of terminological uniformity. The spore-filled "sporangia" of Florideæ, like those of Muscinæ—and in particular of Liverworts—are to be conceived as a separate generation, and, moreover, as a generation springing from cells which have undergone fertilization and have thereby been converted into fruit. The description of the process of fertilization must be postponed to a later section of this book; we have only to notice here that short cells are put forth as branches from the fertilized cells, and that some of these branches abjoint clusters of spores whilst the others develop into a sheath enveloping the assemblage of spores thus produced.

Under the name of Thallophytes are included all such plants as are destitute of vascular bundles and therefore are never developed into real *plant-bodies* (*cf.* vol. i. pp. 590–592). It often happens that Thallophytes form, in addition to the unicellular brood-bodies to which the name of spore must be limited, cell-aggregates which sever themselves from the thallus and become independent, the genesis of



which has not been in any way a result of fertilization. These aggregates of cells are, in a manner, structures intermediate between the unicellular spores and the buds, differentiated into axis and leaves, which occur in vascular plants. They are portions of the thallus which produced them, and are either very like it or assume the same form as soon as their further development is complete. Hence the most appropriate name for these bodies is that of *thallidia* (θαλλός = young shoot; εἶδος = a likeness). They are also known as *gemmae*. Thallidia are some-



Fig. 196.—Thallidia of Muscinæ.

- <sup>1</sup> *Marchantia polymorpha* with cups containing thallidia or gemmæ. <sup>2</sup> Longitudinal section of thallidial or gemmiferous cup. <sup>3</sup> A single thallidium. <sup>4</sup> *Tetraphis pellucida*. <sup>5</sup> A stem of *Tetraphis* bearing a cup containing thallidia. <sup>6</sup> Longitudinal section of a thallidial cup. <sup>7</sup>, <sup>8</sup> Isolated thallidia of *Tetraphis*. <sup>9</sup> A stem of *Leucodon sciurioides* with brood-bodies. <sup>10</sup> A brood-body set free from the stem. <sup>11</sup> Development of a brood-body from the rhizoids of a leaflet torn from *Campylopus fragilis*. <sup>12</sup>, <sup>13</sup>, <sup>14</sup> Development of thallidia at the apex of a leaf of *Syrrhopodon scaber*. <sup>15</sup> *Aulacomnion androgynum*. <sup>16</sup> A stem of the same bearing thallidia. <sup>17</sup>, <sup>18</sup> Single isolated thallidia. <sup>1</sup> natural size; <sup>4</sup>, <sup>15</sup>  $\times 2$ ; <sup>2</sup>, <sup>12</sup>, <sup>18</sup>  $\times$  from 8 to 15; <sup>5</sup>, <sup>6</sup>, <sup>9</sup>, <sup>10</sup>, <sup>14</sup>  $\times$  from 20 to 40; <sup>3</sup>, <sup>7</sup>, <sup>8</sup>, <sup>17</sup>, <sup>18</sup>  $\times 120$ .

times in the form of rows of cells, as, for example, those developed on the leaflets of the Moss *Syrrhopodon scaber* (see figs. 196 <sup>12</sup>, <sup>13</sup>, <sup>14</sup>); sometimes they are nets, as in the Water-Net (*Hydrodictyon*, see figs. 197 <sup>1</sup>, <sup>4</sup>, <sup>5</sup>). In the Moss *Tetraphis pellucida* (see figs. 196 <sup>4</sup>, <sup>5</sup>, <sup>6</sup>, <sup>7</sup>, <sup>8</sup>) they occur as plates of cells, and in other cases they assume the form of globular or ellipsoidal lumps of tissue, as, for instance, in the Moss *Aulacomnion androgynum* (see fig. 196 <sup>15</sup>, <sup>16</sup>, <sup>17</sup>, <sup>18</sup>). Sometimes the number of cells associated

in a brood-body of the kind is limited to two, as is the case in the so-called "teleutospores" of the Rust-Fungus; whilst those of Florideæ sometimes have four cells and are known as "tetraspores". Again, in other cases hundreds of cells are associated together to form a thallidium, an instance of which is afforded by the brood-body or gemma of *Marchantia* (see fig. 196<sup>1,2,3</sup>). The "soredia" of Lichens must also be brought under this head—by the term soredia being understood certain bodies which arise upon the thalli of Lichens and consist of one or more green cells wrapped in a net-work of colourless hyphæ (see vol. i. p. 248).

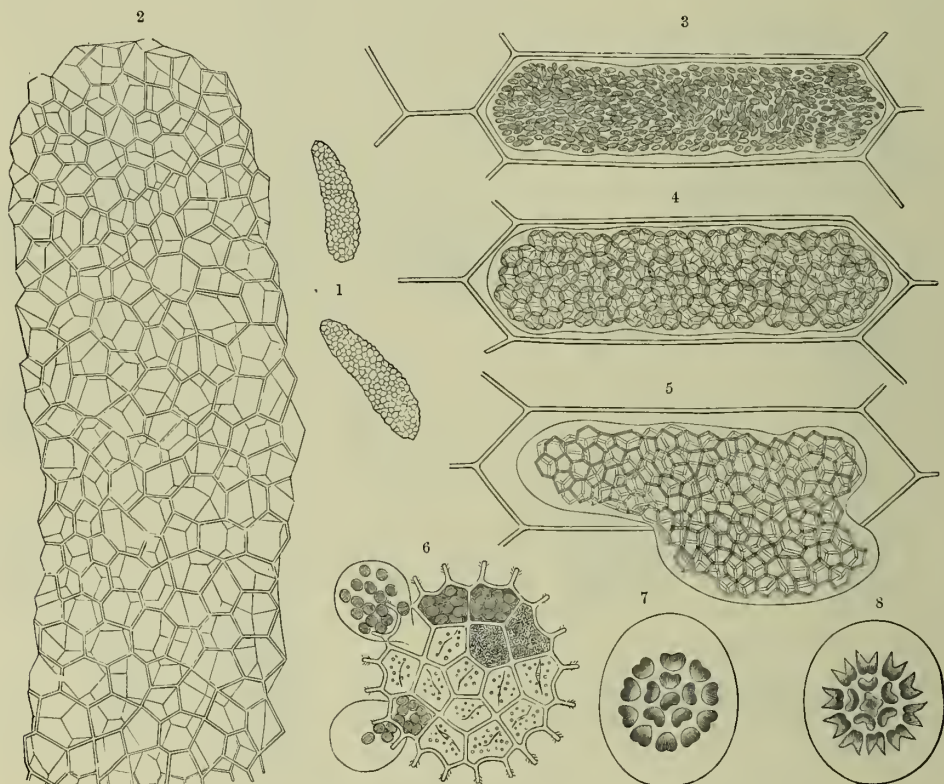


Fig. 197.—Formation of Thallidia in the cells of *Hydrodictyon* and in those of *Pediatrum*.

<sup>1</sup> Water-Net (*Hydrodictyon utriculosum*), natural size. <sup>2</sup> A piece of the Water-Net;  $\times 50$ . <sup>3, 4, 5</sup> Development and escape of a reticulate thallidium;  $\times 300$ . <sup>6</sup> *Pediatrum granulatum*; development and escape of thallidia; the lightly-dotted cell chambers already vacated. <sup>7, 8</sup> Thallidia of *Pediatrum* after their escape;  $\times 240$ .

Thallidia may originate in the interior of a cell-cavity of the parent-plant and escape in the form of complete, though extremely minute, cell-aggregates. Instances of this are afforded by the Water-Net (*Hydrodictyon utriculosum*), which is shown in fig. 197<sup>5</sup>, and by *Pediatrum granulatum* (fig. 197<sup>6</sup>), an organism of frequent occurrence in pools. The alternative method of formation of thallidia is by the severance of groups of superficial cells, which, after an interval of peregrination of variable duration, fasten on to some spot or other and found a new colony. In many Liverworts and Mosses special pockets and

cups are produced, within which thallidia are continuously developed in the manner shown in figs. 196<sup>1, 2, 3, 4, 5, 6, 7, 8</sup>.

The formation of these brood-bodies by Lichens and Mosses may be induced by wounds or mutilations affecting the plants in question; but the stimulus is not here susceptible of being so clearly and surely inferred from its effects—and perhaps has hardly yet been so carefully investigated—as in the case of trees, shrubs, and herbs, which, being planted on a large scale, have afforded experience for centuries with the result that the practice of inducing the formation of buds by mutilation and of using them for the purpose of artificial propagation is extremely common in cultivation. Parasitic thallophytes receive an evident stimulus to the formation of brood-bodies upon the death of their hosts. As long as the host-plant is healthy and vigorous the parasites keep their hyphæ and suckers buried within the nutrient tissue. They there consume all there is to consume, increase in size, and thread their way through wood and green tissue in ever-widening circles—but without ever forming brood-bodies. Not until the host is quite exhausted and languishing at death's-door does the parasite, to avoid the danger of perishing with its foster-parent, provide for its departure from the ruin, and it is then in the form of brood-bodies that it escapes from the tissue it has ravaged. Here and there some of the tubular cells grow quickly from the interior of the dying tissue of the host-plant and emerge to the surface through stomata or rotten cell-walls. All the substance contained in the cells of the parasite becomes concentrated at these new foci of formative activity, and here masses of spores and thallidia are developed and abstricted at the very points where most extensive distribution is rendered possible by currents of air and water. Thus, the parasite is resolved into a number of brood-bodies and abandons the mansion which it has brought to destruction.

#### BUDS ON ROOTS.

Just in front of the house in which I am writing there used to stand years ago a great Aspen. The tree was felled, the axe being laid so close to the earth that only a stump projecting a few centimetres above ground was left. In the following spring the stump became the centre of quite a grove of Aspens, slender shoots having pushed through the grass over a large circular area round the stump. At first the shoots appeared one by one, then by dozens, and at last by hundreds at a time. They grew up into trees, and now, instead of the single Aspen, there is a little wood composed of trees which have not sprung from seed, but from the subterranean roots of the felled Aspen. Before the old tree had been deprived of its trunk and foliage its underground roots produced lateral roots only, which grew in a plane beneath and parallel to the surface, and continued to spread so long as they did not encounter any insuperable obstacle. Suddenly there was a change in the processes going on in this root; its formative energy was no longer devoted to the development of lateral roots, but was directed



to the construction of buds from which green leafy shoots sprang up above the surface of the ground.

A forester of the old school, whose attention I drew to the above phenomenon with a view to ascertaining how he would explain it, told me that when the tree was cut down the flow of sap destined for the nourishment of the trunk and its crown of foliage was arrested in the roots underground, and thereupon sought an outlet elsewhere. Lateral roots having become useless, the diverted juices did not form them, but instead sent a great number of delicate shoots above the ground, because this was the only manner of preserving the life of the Aspen. At first sight this may seem to some people a foolish answer, and I have even heard it called absurd. Nevertheless we are obliged, after impartial consideration, to admit that we are not in a position to give any explanation which is not essentially the same. If we conceive the living protoplasts in the formative tissue of the roots as being the "juices" referred to by the forester, there is no longer any difference between his explanation and that given by Science. At the very spots where formerly lateral roots would have been developed, leafy stems are produced. The same protoplasts which now work at the construction of a bud would, if the tree had not been cut down, have fashioned a lateral root. That this alteration in active function was caused by the felling of the tree is certain, although no mechanical explanation of this stimulus can be given. The only possible source of excitation seems to be the checking of the egress of formative material stored in the roots in the direction in which it was formerly accustomed to flow.

Another special point of interest connected with the history of this Aspen is that for the most part the roots, after giving rise to a series of shoots, died and decayed, whilst the shoots developed into separate and independent trees, each furnished with roots of its own, so that they look as if they had been deliberately planted in the earth in rows. As a matter of fact, however, the Aspen itself produced these saplings from its subterranean portions, and planted them out, thus not only renewing its own youth but multiplying. For such multiplication it is evidently necessary that some cell in that part of the root which possesses the power of growth should form the starting-point or rudiment of a new shoot. The cell chosen for the purpose divides into daughter-cells, and these again become subdivided; but several adjacent cells also participate in the new fabrication, and we can picture to ourselves the process as the action of a group of protoplasts located within the limits of the living and formative tissue of the root, which separate themselves off from the rest and form a confederation of mutually helpful associates with the common function of constructing the new shoot. Neither the protoplast in the mother-cell of the young shoot nor the adjacent protoplasts undergo any stimulation by neighbouring cells before beginning their work. No process of pairing takes place. The phenomenon of renewal and multiplication of the Aspen which goes on before our eyes must therefore be classed as a case of asexual reproduction. The fact that a single root of the Aspen, instead of producing one sapling

only, gave rise to ten, obliges us to suppose that these protoplasts of the growing tissue of the root, which separated themselves off under the influence of the new conditions created by the felling of the tree, arranged themselves in ten groups and each group from that time forth devoted itself to the new task of furthering the growth of the shoot developing at its centre. On investigation we find that these aggregations of cells are invariably situated in the deeper layers of the rind. In the first place a delicate tissue is developed from a particular cell which dominates the entire group and governs the process of construction. This tissue pushes outwards, on the one hand, towards the superficial layers of the rind, whilst, on the other hand, it sends a shaft inwards into the cambium layer of the root. Immediately afterwards vascular bundles are developed, and the shaft-like rudiment of the young bud is through them placed in connection with the woody tissue of the root, and when all this is finished the rind is finally broken through, and a bud clothed with leaves behind its growing point bursts out through the opening.

These buds, and the shoots arising from them, are termed radical buds and shoots. They are anything but rare, and it would be an error to suppose that they only occur on the Aspen because that tree has been chosen to illustrate the subject. Not only a great number of trees, but also many shrubs, and a host of herbaceous plants, great and small, exhibit this kind of revival and multiplication, and for many species it is the safest and most fruitful mode of reproduction. It would also be wrong to suppose that radical buds only arise when the aërial parts of the plant concerned have been injured or destroyed in consequence of some unusual occurrence. A shock of the kind is certainly the most frequent cause; but it is equally certain that of trees and shrubs not a few develop rudimentary buds on their roots when their time comes—*i.e.* when they have become decrepit, and one branch after another is dying—without their having suffered any injury from worm or weather, or from the woodman's axe. A profuse after-growth of young plants always springs from the roots and surrounds old and dry trees of the following kinds:—the Aspen (*Populus tremula*), the Tree of Heaven (*Ailanthus glandulosa*), the Tulip-tree (*Liriodendron tulipifera*), and the Osage Orange (*Maclura aurantiaca*), and the same statement applies to the following shrubs when they begin to wither—the Raspberry (*Rubus Idæus*), the Sea-Buckthorn (*Hippophae*), the Hawthorn (*Crataegus*), the Barberry (*Berberis*), the Lilac (*Syringa*), and the Rose (*Rosa*), and to many other woody plants; whereas, no such "breaking" from the root is seen on young specimens of the above unless there has been some previous injury to the parts above ground.

The budding power of roots is made use of by gardeners for the purpose of artificial propagation. They cut pieces from the roots of the plants they wish to multiply and insert them in soil which is kept moist, and they may then count almost with certainty upon the development of several buds on each separate piece of root. This mode of propagation by root-cuttings or slips, as they are called, is attended by particularly successful results when applied to the flowering trees or shrubs of *Cydonia Japonica*, *Paulownia imperialis*, *Tecoma radicans*, *Dais coto-*

*folia*, and to various species of *Acacia*, *Halesia*, *Hermannia*, and *Plumbago*. Moreover, the development of buds on roots is observed to take place not only in trees and shrubs, but also in herbaceous plants; and, indeed, in some it is of regular, annual recurrence. As instances of this may be mentioned the Dwarf Elder (*Sambucus Ebulus*), *Asclepias Cornuti*, *Sophora alopecuroides*, *Lepidium latifolium*, the Dock (*Rumex Acetosella*), various species of the Toad-flax and Spurge (e.g. *Linaria pallida*, *L. genistæfolia*, *L. vulgaris*, *Euphorbia Cyparissias*), and several Composites and Pelargoniums. In another series of herbaceous plants the phenomenon occurs exceptionally as a result of special external conditions, and chiefly in consequence of injuries, as, for example, in case of damage to the roots of certain Orchids (*Epipactis microphylla*, *Neottia Nidus-avis*), or of the Adder's Tongue amongst Ferns (*Ophioglossum vulgare*). Nor must we omit to mention the buds which are formed on aerial roots. There is so regular a production of buds from the columnar aerial roots of tropical Fig-trees, and of leafy shoots from the buds thus developed, that at first sight one is inclined to take the root-columns for trunks.

#### BUDS ON STEMS.

Buds and shoots growing directly from a part of the stem are termed cauline buds and shoots. Any part of a stem may become the point of inception of a bud. The commonest positions occupied by buds are the regions of the stem which bear respectively scale-leaves and foliage-leaves, and this is especially the case with those buds which subsequently become brood-bodies. But also lower down and higher up buds are observed to develop, and do so, indeed, without the occurrence of any apparent injury or other assignable external cause. Thus, for instance, it frequently happens that buds are developed on the hypocotyl of the Scarlet Pimpernel (*Anagallis arvensis*), which abounds in our fields and kitchen-gardens, and the same is true of the species of Spurge (*Euphorbia Peplus* and *E. vulgaris*) which grow as weeds in company with the Pimpernel, and likewise of young Toad-flax plants (*Linaria vulgaris*), and of a few Umbellifers. These buds grow out immediately into green leafy shoots. In all probability the phenomenon occurs in many other plants besides, but hitherto the subject has received only cursory attention.

These buds on the hypocotyl are all the more worthy of notice because they emerge below the cotyledons and in no case from a leaf-axil, *i.e.* the angle formed by a leaf with the stem. In the region of the foliage-leaves it is comparatively rare for a bud to originate at any other spot than in the axil of a leaf. As instances may be mentioned the extra-axillary buds of the Nightshades (Solanaceae), the buds in *Serjania*, *Medeola asparagoides*, &c., which spring laterally from the stem close to the foliage-leaves, and those in the Vine and Virginian Creeper (Ampelideæ), which are set opposite to the foliage-leaves. But even in these cases the positions of the buds, relative to the foliage-leaves of the stem, are always such as to be most naturally explained by the need of the former to obtain the formative materials produced in the green tissue of the leaves, in order to complete their own develop-



ment; and these materials are most directly conveyed to them if they are situated as near as possible to the spot where the vascular bundles of a green leaf lead into the stem.

When a large number of foliage-leaves are packed closely together upon a stem, it is scarcely possible for a bud to be developed in every axil. On such occasions the buds appear always to possess the power of selecting the most convenient points of origin. The majority of leaf-axils are altogether destitute of buds, and it is only at spots where their inception would be most favourable to the plant's development that a few hardy buds are put forth. This is what happens, for example, in most species of Spurge, in the Toad-flax, in Pines and Firs, in Araucarias, and the rest of the numerous family of Conifers. Where buds are formed in the axils of leaves, either there is one to each leaf, or several are crowded together in an axil, and of these one is conspicuous owing to its central position, and also usually for its size, whilst the rest are subordinate. The occurrence on the leafy region of the stem of buds crowded together in this fashion—the meaning of which will be examined in detail in the next few pages—is confined to certain species belonging to the Flora of the Mediterranean, of Australia, and of various Steppe-lands. They are much more commonly found on such regions of the stem as bear scale-leaves, especially in bulbous plants, which sometimes exhibit as many as a dozen little buds springing from the short, thick stem in the axil of one of the expanded scaly leaves of the bulb.

The buds produced in the floral region of the stem (or inflorescence) usually develop into flowers, and their function being the production of fruit, they cannot be considered until a later section of this work is reached. Meanwhile the bud-form of brood-body is not entirely absent from this region of the stem. Grasses, Saxifrages, and Polygonums afford a great number of examples of their occurrence in that position.

A wound may cause the formation of a bud at any altitude upon the stem. The bud invariably springs from the injured spot and often no relation can be detected between its point of insertion and the position of the leaves. An instance is known where the herbaceous stem of a Sea-Kale (*Crambe maritima*) was cut through transversely, and, after the pith had decayed, buds were formed on the inner surface of the vascular-bundle ring from the tissue of the so-called vascular-bundle sheath, and from the buds shoots eventually developed. If the main trunk or a branch of an Angiospermous tree, such as an Oak or Ash, is cut off smooth, a mass of tissue is formed from the cambium, thus exposed, at the boundary between wood and bast; this tissue gradually creeps out from the margins of the wound and swelling up takes on the form of a circular rampart. The wood-cells which have been cut through and left bare within the circumference of the rampart have not the power of dividing and multiplying so as to initiate a new structure, but are dried up by exposure to the air and perish. The tissue forming the rampart continues, however, to increase in breadth, and encroaches upon the dead interior of the section of the stump so completely that the cut surface of wood

is quite covered over by the new growth. The latter is termed "callus", and may be compared to the tissue which is developed when an arm or a foot is amputated, and which grows from the ligaments beneath the skin until it gradually covers the whole stump. The callus in plants derives a special interest from the fact that within it are formed the rudiments of fresh buds, from which subsequently spring the shoots which "break" so plentifully. A longitudinal section through an Oak stump thus overgrown shows the callus wedged, as it were, between the old bast and the old wood; and we find that it consists of cork and parenchymatous cells, whilst vascular tissues, springing from the wedged portion of the callus, have also been developed, and, descending in bent and tortuous lines, establish an organic connection with the old trunk. The buds arising in the callus do not stand in any relation of any sort to the leaves, as has already been mentioned; nor do the intervals between them follow a geometric law, as is the case with the buds which take their rise from the axils of leaves. They are for the most part in aggregations and are produced anything but simultaneously. A callus of the kind may continue to produce buds at appropriate spots year after year, and shoots of many different ages may be seen springing from it. One cannot contemplate such a callus growth, covering a stump and sending out shoots as direct off-shoots of the decapitated trunk, without being involuntarily reminded of trees that have been "ennobled" by grafting in the manner described in vol. i. pp. 213, 214. There is also an analogy to certain parasitic plants, such as *Loranthus*, in which the connection with the host is established in exactly the same way as that between callus-buds and tree-stump by means of a tissue interposed between wood and bark (*cf.* vol. i. p. 211).

A formation of callus ensues upon the excision of the cortex from the side of a stem in the same manner as when the entire trunk is sawn through; and the process of covering up the exposed wood with callus, derived from the tissue lying between the bark and the wood, goes on similarly in the case of lateral injuries to the trunk. Some trees in addition exhibit a formation of callus without external damage having been received, as, for instance, the Ash, which has a bark liable to split and break open here and there spontaneously, whereupon a tissue of the nature of callus is formed in the open places. Oldish trunks of the North-American Ash (*Fraxinus nana*) are invariably covered with swellings and callosities of the kind, and most of them furnish starting-points for a score or more of buds.

The buds which spring from growths of callus on trunks must not be confounded with those called by foresters "dormant eyes" and "dormant buds". Nor must we fail to distinguish them from the structures which have been termed superposed and collateral buds, which whilst exhibiting extreme diversity in their various modes of development, yet all constitute contrivances for the preservation of the plants from destruction in that their function is to replace dead shoots. With reference to the part played by these structures, it is most convenient to classify them under the name of "reserve-buds". They either originate simultaneously with those which they are destined in certain circumstances to replace, or they

are only subsequently formed in the cortex in the immediate neighbourhood of the points of origin of shoots which have already withered. The latter is of comparatively rare occurrence. In *Spartium scoparium*, which is represented in vol. i. p. 331, one bud only is produced in each axil. The following year, this bud grows out into a long switch, and at the same time a new bud is initiated in the cortical tissue just beneath the base of this shoot. If the first shoot dies next year, as often happens, especially in the case of plants growing near the northern limit of the Mediterranean region, the second bud produces a shoot, and close under its base is formed once more the rudiment of a bud for future substitution. This may go on for several years until at last a whole row of withered stumps are to be seen above the last substituted shoot. This mode of growth, which has been observed not only in *Spartium*, but also in several allied Papilionaceæ belonging to the Mediterranean Flora, is very prejudicial to the freshness and vigour of the plant's appearance. The presence of a number of withered remnants crowded together produces an impression of disease and starvation; else, as an alternative, one is tempted to suppose that the bushes have been cropped by cattle, or annually truncated by man, whereas they themselves accomplish all these changes without any damage of the kind being inflicted.

In *Robinia Pseudacacia*, the plant known by the name of Acacia, a single bud is formed at first in the axil of each foliage-leaf. But later on the stem close to the thickened base of the petiole becomes hollowed out, and in the cavity thus formed little knobs arise underneath the first bud. Sometimes there is one only, sometimes there are two or even three. These knobs are nothing more or less than first rudiments of reserve-buds which develop in this position where they are sheltered and protected by the remaining portion of the petiole. If, as is often the case, in the following year the shoot put forth by the first bud dies, it falls to the uppermost reserve-bud to develop into a substitution-shoot, which may perish in its turn and be replaced by the next reserve-bud. The different species of the genus *Gleditschia* behave in precisely the same way as *Robinia Pseudacacia*, but in them the reserve-buds are only partially hidden beneath the remnant of petiole, and the power of forming new buds at the ends of the branches is here almost unlimited. In some species of *Gleditschia*, e.g. *G. Caspica*, a substitution of shoots, one for another, as they successively dry up, takes place for a period of ten or more years. The consequence is that the long branches of these trees are nodulated at the seats of origin of the buds, and the dried stumps of upwards of twenty short branches dating from previous years are seen crowded close together on these nodes.

In *Pterocarya Caucasica*, a Caucasian tree allied to the Walnut, a single bud is formed every year in the axil of each foliage-leaf, and this bud has the peculiarity of being elevated from 1.5 cm. to 2 cm. above the leaf-insertion. Whilst it is growing next year into a shoot, the rudiment of a reserve-bud is formed just above the original leaf-insertion, but it only develops in some subsequent year in the event of injury to the first shoot.

Far more common than the above are the cases where the buds which sprout in



the first year and those which remain dormant until called upon to replace the earlier ones originate all together simultaneously. In the Common Elder (*Sambucus nigra*) two buds are formed one above the other in each leaf-axil; in the blue-berried Honeysuckle (*Lonicera cærulea*) and in several of its allied species, three buds of almost equal size are superimposed one above another in a straight line in each axil. In the year following their formation, usually only one of them grows out into a shoot; the others stop as they are, and maintain their vitality for a couple of years in reserve and only then develop if the first shoot has met with destruction. The North-American False Indigo, species of which (*e.g.* *Amorpha fruticosa*, *A. glauca*, and *A. nana*) are cultivated as ornamental shrubs in European gardens, produces two buds of different sizes above each foliage-leaf, the larger of the two being placed just above the smaller. The former sends forth a shoot in the following year, the latter remains in reserve. If the shoot first developed withers, as very often happens, the reserve-bud sprouts, and the withered stump of the first shoot is then visible just above the fresh one. The North-American tree *Gymnocladus Canadensis* also exhibits on the upper ramifications of its powerful branches two superimposed buds above the insertion of each leaf; the larger is situated above the smaller, and the latter only develops into a shoot in the event of its being required as a substitute. Several other woody plants which, though their stems become very thick, possess neither the growth of a tree nor a symmetrical crown of foliage—such as the Judas-tree (*Cercis Siliquastrum*) and the *Forsythia viridissima* of Japan—put forth long switch-like shoots, the upper halves of which often die off during the winter. The buds on the lower surviving half of each shoot are very close together, and generally they are in pairs, the upper one in each pair being close upon the lower. Only the upper one of a pair is at first developed in the next year; the lower bud does not develop unless the other fails.

It is sometimes the case that the axil of every leaf produces three buds set side by side instead of one above another. The middle bud sends out a shoot in the following year whilst the lateral ones are left as a reserve. The year after, if the shoot has died, what happens is either that one of the two accessory buds develops—as, for example, in *Lonicera fragrantissima* and in the case of the long shoots of the Nettle-trees (*Celtis Tournefortii*, *C. orientalis*, *C. occidentalis*), or both accessory buds develop simultaneously—as in the Southern Reed (*Arundo Donax*) and in several species of the genus *Bambusa*. The species belonging to the genus *Zanthoxylon* form in each leaf-axil the rudiments of from nine to eighteen buds, of which the middle one is the biggest and grows out during the following year into a short or long shoot. The other smaller buds are kept in reserve in the cortex at the base of the shoot.

In the Tree of Chastity (*Vitex Agnus-castus*) four buds are set in the axil of each foliage-leaf. The central bud is the largest and a smaller one is situated underneath it, whilst the other two—also smaller—are posted to the right and left respectively of the first. Next year a shoot is put forth from the large central bud whilst

the other three remain dormant. By the second year this shoot has probably perished, and in that case the little reserve-buds sprout. Their development is not infrequently simultaneous, so that here and there upon the tree we have tufts, each consisting of four slender shoots—one withered and three green—which all radiate from one point. If the three later shoots dry off at the ends, the buds on their basal parts produce fresh shoots, and the bushes present a bristly and not very ornamental appearance like besoms, especially when they are destitute of foliage.

A curious development of reserve-buds may also be observed in *Atraphaxis*, a ragged shrub indigenous to the Steppes of Southern Russia. Four buds are formed simultaneously and in close proximity to one another in the axil of every foliage-leaf. Of these a very small one is immediately above the insertion of the leaf; it has a large one above, and two of medium size on either side of it. The large bud becomes a leafy shoot and the small one a blossom. The two lateral buds are kept in reserve unchanged during the second year, and in some circumstances during the third also. If the shoot dies, the development of the lateral reserve-buds is proceeded with; but as soon as they begin to sprout, the rudiments of fresh reserve-buds are formed in the cortex to the right and left of those that are thus developing. Here again, the ragged habit of growth of the shrub is connected with its peculiar mode of bud-formation. The following case is also very common. Of a crowd of axillary buds, placed either side by side or one upon another, one or more produce flowering shoots. When the fruits generated in the flowers have dropped—an event in this connection equivalent to the fall of the shoots which bear them—and the spots of detachment are scarred over, the reserve-buds come into play for the first time. In *Spiræa crenata* there is only one such reserve-bud; in the Dwarf Almond (*Amygdalus nana*) and the Mahaleb (*Prunus Mahaleb*) there are two or three. The diversity amongst plants in this respect is almost endless, but the compass of this work does not admit of the subject being treated in greater detail. Seeing, however, that the facts involved have not received due consideration on the part of botanists, I should like to draw attention to the peculiar phenomena of development in *Buddleia*, *Rhodotypus*, *Fontanesia*, *Philadelphus*, *Rubus*, *Berberis*, *Caragana*, *Alhagi*, *Lycium*, and *Ephedra*, and also to point out that amongst woody, shrubby and suffruticose Steppe-plants, which are especially liable to frost-bite and desiccation, many exhibit highly interesting characteristics in their development of reserve-buds.

In Willows we find a form of reserve-bud which differs from all the rest. It is obvious at a glance that every bud on an annual shoot of a Willow is entirely shrouded by a single scale shaped like a hood. This bud-scale originates in the outer layers of the cortical tissue, and is, so to speak, a raised piece of the cortex covering the rudimentary bud. The large bud wrapped in this scale possesses an axis which has arisen laterally from the axis of the branch which bears the bud, and the vessels and cells of the wood may be followed uninterruptedly from the branch to the base of the bud. But, close to the latter, we also notice some very small bud-rudiments with no bundles running into them from the branch. They take their

rise in a special cellular tissue intercalated in the cortex, and on a branch in its first year are not externally visible, because they are covered by the large hood-shaped scale. The tissue of cells from which these small buds spring might be compared to a callus if it were not produced on wholly uninjured branches and long before the formation of cracks and fissures in the bark. In the second year, when the large central bud begins to produce a lateral branch, throwing off the hood-scale and elongating its axis, the small buds also become visible in the form of spherical or oval knobs at the base of the new side-branch springing from the large bud. They do not, however, get larger or smaller, but remain completely dormant and unaltered. There is even a possibility of their never developing further, but in the event of the branch at the base of which they were produced receiving an injury and dying, they are aroused from their lethargy and grow out into leafy ramifications. It is obviously their function to replace such of their predecessors as fall victims to unfavourable external conditions.

The Crack-Willows derive their name from the extraordinary fragility of their branches. The hard bast and wood at the base of their one-year-old and two-year-old branches exhibit a peculiar structure, the result of which is that a slight shock is sufficient to sever the tissue, so that the branch breaks across at its base and drops off. It seems to be an advantage for these Crack-Willows to get rid of certain leafless and useless twigs which bear nothing but the scars of shed catkins, and are merely an encumbrance. Thus much is certain, that several kinds of Crack-Willow cast off spontaneously a number of these branches, and that the buds above described as lying dormant in the cortex put forth leafy shoots as substitutes. Similar phenomena may be observed in Poplars. But in them the twigs break off at a little distance from the base, and the substitution of green, leafy branches for those covered with dead excrescences is effected by means of reserve-buds performed in the axils of former bud-scales. There can be no question of mutilation in these cases any more than in the autumnal shedding of leaves which takes place spontaneously for the benefit of the plants concerned, and is not susceptible to the influence of external conditions except inasmuch as the latter may accelerate or retard it.

In all the cases hitherto described, the substitution-buds are developed in the cortical tissue. At first, there is no direct connection between them and the woody tissue of the stem; it is only when these buds are roused from their lethargy, and called upon to put forth shoots, to replace anterior or collateral shoots which have fallen, that communication with the wood, and to that extent also with the current of crude sap, is set up by means of special conductive strands.

There is, however, another form of accessory bud, which is connected from the very beginning with the wood of the stem appertaining to it, and maintains this during its whole life. In forestry the name of "dormant eye" already referred to is employed in particular for this form of bud. If a year-old branch is examined, it is found that the buds in the leaf-axils of its upper half are strikingly larger and more vigorous than those near the base; indeed, above the point of insertion of the



lowest scale-leaves of the branch, it is not even possible in most cases to detect so much as a swelling that might be construed into the rudiment of a new bud. It is not till a longitudinal section is made through the lowest part of the branch that one perceives the existence of buds, here, too, in a very rudimentary condition and buried in the cortical tissue. The large buds to be seen at the close of the first year about the middle and at the extremity of the branch develop next year into fresh branches, the lower parts of which are again clothed with bud-scales, and the upper parts with foliage-leaves; but the small, inconspicuous or invisible buds at the base of the first year's shoot are left undeveloped and completely dormant. They are preserved practically unaltered in size or shape at the spots where they originated within the cortex, in some cases showing above the surface, in others concealed by the outer coats of the bark; and the only change which takes place is that the bundles leading from the wood of the branch to the dormant buds elongate yearly to the extent of the thickness of the new woody ring. These bundles exhibit the same disposition as those within the shoots which are visible on the surface, and so far, we might look upon them as latent lateral axes or side branches imbedded in the wood of the main branch and terminating in dormant buds. The analogy is confirmed by the fact that the lateral axes buried in the wood are capable of ramifying in the same manner as those which project beyond the periphery of the stem and send their branches out into the air. The rudiments of fresh buds may also be formed on the concealed branchlets within the wood of the continually thickening main axis; and in many trees densely-branched structures terminating in dormant buds are formed in the wood of the stem, and exercise a disturbing influence on the course of the surrounding tubes and fibres of the wood of the main stem, causing them to bend and twist about to a very great extent. In this manner knobs of various sizes are formed, composed of the branched latent shoots which terminate in dormant buds and of winding wood-fibres. These nodules are found interspersed amongst the elements of the wood, which pursue a normal course, and they are known as "bird's eyes". Sections of such bird's-eye timber were much in demand some decades ago for use as veneering in cabinet-making, owing to the curious traceries exhibited by them, which usually take the form of eyes surrounded by rings and of serpentine lines—the former corresponding to latent branches, the latter to sinuous wood-fibres.

As already mentioned, in many trees and shrubs it is particularly the buds pertaining to the axils of the lowest leaf-structures that are kept back in a dormant condition. A striking deviation from this habit is exhibited by the Tamarisks (*Tamarix*). The young branches, covered with innumerable little leaves and an assemblage of buds—usually three in number—are formed in the axil of each leaf. Want of space would of itself be sufficient to make it impossible that all these buds should produce shoots in the following year and develop simultaneously; about a thousand lateral branches would in that case be produced simultaneously from an axis little over a metre in length. As a matter of fact only comparatively few of the buds produce shoots, and these are so aptly distributed that no one of them

restricts the freedom of another by pushing it aside or competing for its supply of air and light. Hundreds of rudimentary buds, not only at the base but scattered over the entire length of the branch, remain dormant in the Tamarisk branch, as it grows thicker and thicker, and thus is explained the fact that shoots springing from such branches have an almost inexhaustible store of lateral shoots, and are capable of producing every year afterwards hundreds of fresh shoots.

Those reserve-buds which are formed in the cortical tissue and have no connection with the wood of the stem which bears them, for the most part maintain their vitality only for a few years. The dormant buds at the extremities of latent branches may, on the other hand, preserve their capacity for development for many years, although they undergo no change either in shape or in size. No doubt many of them die in the course of a year or two without being replaced by others; whilst many others which perish have their places filled by new ones developed at the ends of embedded branches. But these are rare occurrences in comparison with the large number of cases where dormant buds retain their vitality for many years.

Suppose the case of a tree one hundred years old, which has been shattered by a violent storm. With its crown of foliage torn down and its great branches broken off and strewn upon the ground, it reminds one of the ruins of a building of which roof, gables, battlements, and walls have been partially demolished. Where previously thousands of leafy boughs formed a spreading crown, now a few riven stumps are seen standing in dreary solitude. The tree has the appearance of being hopelessly destroyed, and one would anticipate that its trunk would dry up completely in the following year. Yet, marvellous to relate, fresh life quickens in the old and shattered trunk. Buds which have lain dormant in the cortex during scores of years stretch out, push their way through the fissures in the bark and develop into vigorous branches, and within a twelvemonth the thick stumps of the old trunk and branches are covered over with a drapery of fresh shoots which have buds set in the axils of their leaves. After another year has passed lateral branches develop from some of these buds, and this process continues until, in about ten years, the maimed tree becomes furnished with a new, densely-ramifying crown of foliage. Who, after witnessing such a phenomenon as this, can doubt that the arrested development of a portion of the cauline buds is an adaptation to ensure trees and shrubs against destruction in case of their being fractured by the wind or otherwise mutilated, or that dormant buds are to be looked upon as a reserve to meet possible accidents in the future!

The fact that twigs which have shed themselves or succumbed to adverse external influences are replaced out of the store of dormant buds or by the buds of the callus, has led to various interferences on the part of man with the natural growth of cultivated plants, and has given rise to a whole series of methods of propagation, which have been employed by farmers and foresters ever since ancient times. To this class of operations belongs, for example, the method employed to promote the growth of underwood, which mainly depends on the development

upon the stumps left when the wood is cut, of new shoots from the callus or from the dormant eyes, shoots which in the course of thirty or forty years replace the old plantation, that is to say, the mass of wood which has been taken away. Pollarding is another instance. Pollard-trees are kept cut down to a particular height, and in consequence become thickened at the top, as may be seen in the case of Poplars, Ashes, and more particularly Willows. The pruning of Vines and Fruit-trees is likewise of this category, and the same process is applied also to the woody plants trained to form espaliers or hedges when a park is being laid down or an estate inclosed. All these manipulations have in view, on the one hand, a development of more vigorous shoots from the stumps that are left behind and the acquisition of as abundant a yield of timber, forage, or fruit as possible; on the other hand, a denser growth of the tree-top, or a stunting of the tree, such as is required for gardens in the old French style, with their formal green walls, obelisks, and marvellous ornamentation. Seeing, however, that each of the various trees and shrubs has peculiarities of its own in relation to the formation of callus and dormant eyes, many different modes of pruning are applied to them. We cannot generalize from one case to all the rest, and it would be a great mistake, for example, to try to pollard Apple-trees like Willows, or to convert Pines into under-wood. Climatic conditions must also be taken into account in connection with these intentional mutilations of cultivated plants. To give one instance of their effect, it may be mentioned that vine-pruning in Hungarian vineyards is quite different from the corresponding process employed on the Rhine, whilst the latter again differs from the method practised in Northern Italy, which, in its turn, is not the same as that of Southern Italy. In each locality the kind of treatment most adapted to prevailing climatic conditions has been found out in course of time.

#### BUDS ON LEAVES.

Hitherto only such buds as are developed on roots or on the various regions of the stem have been dealt with; but an enumeration of these does not nearly exhaust the multiplicity of bud-forms which exist. Buds and shoots may also spring from the tissues of leaves—particularly foliage-leaves. These are termed epiphyllous buds or shoots, and they are classified in several groups according to their places of origin.

Before discussing this classification it is necessary to note carefully that epiphyllous buds must be strictly distinguished from those which occur on the foliage-leaves of *Helwingia* and on the leaf-like cladodes (or phylloclades) of Butcher's-broom, &c. As regards *Helwingia* (see fig. 198) careful investigations prove that certain strands proceed from the leaf-bearing axis to the buds seated upon the leaves. Each of these strands represents a lateral axis, but instead of being free it is bound up (or fused) with the midrib of the leaf from the axil of which it springs. The lateral axis thus adnate to the midrib first abandons its connection with the latter at a spot on the lamina, about a third of its entire



length from the base. It there terminates in a bud, or, if it divides, in several buds, and inasmuch as these are flower-buds, it may be looked upon as a flower-stalk. These buds cannot therefore be said to be epiphyllous, *i.e.* to spring direct from the tissue of a foliage-leaf. In reality each is borne upon a structure of the nature of a stem, only the peduncle, stalk, or axis has partially coalesced with the midrib of a leaf. Willdenow, who was the first to describe it, named the plant, represented in fig. 198, the Butcher's-broom *Helwingia rusciflora*,



Fig. 198. — *Helwingia rusciflora*, with flowers seated upon the foliage-leaves.

because the floral buds here as in the Butcher's-broom (*Ruscus*) were borne by foliaceous structures (*cf.* vol. i. p. 333). The two cases are, however, essentially different. The green leaf-like structures in the Butcher's-broom, which carry floral buds upon their upper surfaces, are not leaves at all, but leaf-like shoots, that is to say axes, and the buds upon them are, therefore, not epiphyllous but cauline. The same statement applies, of course, to other plants with flat, expanded shoots, a few representatives of which are shown in the illustration of p. 335 of the first volume, and in this category must be included Ferns also, if we look upon their fronds as phylloclades, and not as foliage-leaves. It would be quite out of place here to enter into the question of the nature of fern-fronds, or to set forth the reasons why they must be considered as phylloclades. The proof cannot be

conveniently introduced until we come to the description of Ferns themselves. It is sufficient to mention here that buds very frequently occur on the fronds of Ferns; indeed, certain species, e.g. *Asplenium bulbiferum* (see fig. 200) develop buds on almost all their fronds. In most cases they spring from the surface of the green pinnæ, but in *Ceratopteris thalictroides*, a common denizen of swamps in the East Indies, it is from the little stalks of the ultimate green lobes, in

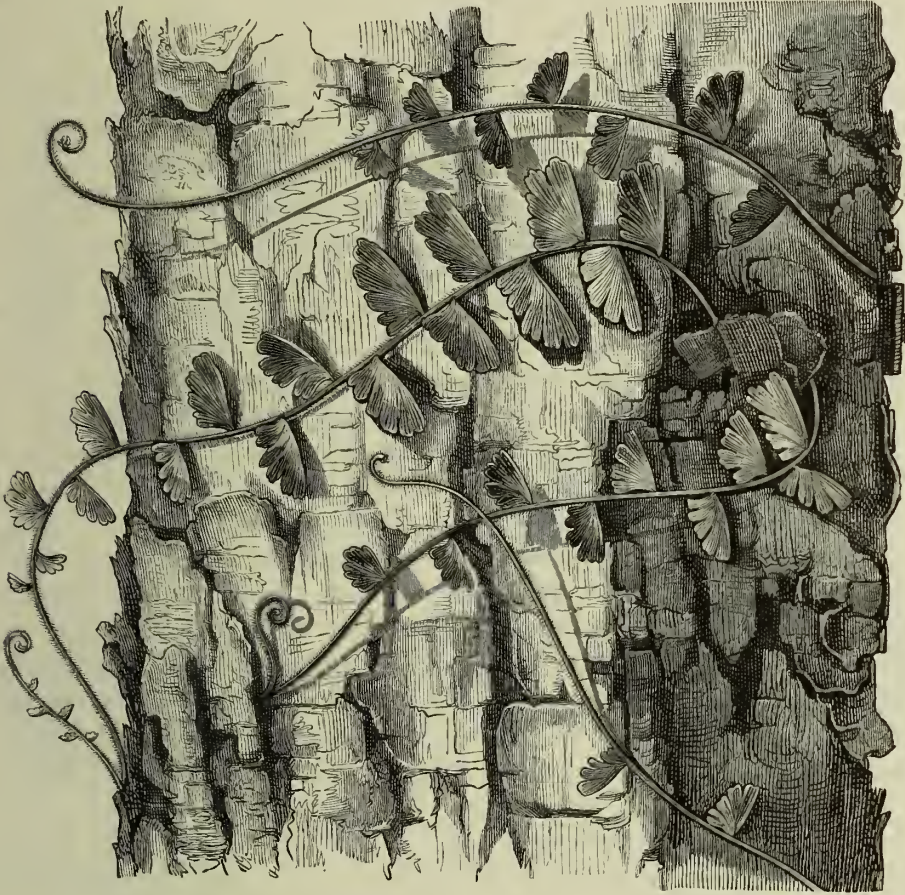


Fig. 199.—Formation of Buds on the apices of the Fronds of Ferns: *Asplenium Edgeworthii*.

*Gleichenia* from the angles of the forkings of the fronds (cf. fig. 189<sup>6</sup>), and in *Asplenium Edgeworthii* (see fig. 199), from the apices of the fronds, that is to say from the extremities of the cladodes. The last-mentioned Fern grows upon the bark of trees, and the tips of its fronds are endowed with the property of avoiding the light, in other words, they bend towards the darkest parts of their substratum, creeping into the fissures in the bark, where they become firmly adnate, and each develops a bud above the point of contact. This bud gives rise once more to fronds, of which, however, one only, as a rule, develops vigorously. After it has unrolled itself, this new frond in turn searches with its apex for a dark rift. The



process is repeated over and over again, and results in the trees, upon the bark of which the *Asplenium* has established itself, being regularly encircled and woven over by fronds, as is shown in fig. 199. The separate fronds of the fern in such circumstances have a strong resemblance to the runners of certain species of *Veronica*, *Ajuga*, and Periwinkle, which have their leaves arranged in two rows.

Unlike the above cases—viz. the buds of *Helwingia* borne on special stalks adherent to the leaves, those growing on the cladodes of the Butcher's-broom, and those on the fronds of Ferns, all of which must, in spite of their extreme similarity to epiphyllous buds, be looked upon as cauline—true epiphyllous buds always arise from cells of a true leaf and have no connection with adjacent axes beyond that involved in the fact of the bud-producing leaf being derived like all other leaves from a stem. Epiphyllous buds are even produced by leaves severed from the axis; indeed, in many instances, the severance of the leaves is itself the apparent cause of the development of the buds. This phenomenon is exhibited, for example, by *Bryophyllum calicinum*, a plant of the House-leek family which belongs to the tropical parts of the Old World, but has long been cultivated in our greenhouses and has attained a certain celebrity even in non-scientific circles, owing to the fact that Goethe interested himself in it and mentions it repeatedly in his writings. The foliage-leaves of this *Bryophyllum* (see fig. 200<sup>3</sup>) are deeply divided, the separate lobes being oblong-obovate and conspicuously notched. Every full-sized leaf exhibits in each notch of the margin a group of cells, which is perceptible as a dot to the naked eye. So long as the leaf remains upon the stem there is usually no further development of these cell-aggregates, but if the leaf is plucked off and laid on the earth an active process of division is set up in them, the result of which is the formation of a little plant with stem, leaves, and roots, as is represented in the figure opposite. The leaves of *Bryophyllum calicinum* are thick and fleshy, and contain when mature such an abundance of reserve material and water as to render it superfluous that any absorption of nutriment from the environment should take place. It is not till later that the little plants which spring from the notches of the leaf, having used up the materials stored in the latter, are driven to seek food from the environment by means of their roots. If the leaf has been laid on moderately damp earth, the rootlets of the young plants, developed in its notches, penetrate the ground and, in the event of the tissue of the leaf being in the meantime exhausted and withered, all the little plants become independent and develop into full-sized individuals. Phenomena similar to those exhibited by *Bryophyllum calicinum* are also observed in other plants with thick, fleshy leaves, particularly in *Echeverias*. Young plants also make their appearance sometimes on the fleshy leaves of *Rochea falcata* after they have been picked. There is, it is true, the noteworthy difference that the phenomenon is not foreshadowed, as in *Bryophyllum*, by the existence of special groups of cells at the points of origin; but *Bryophyllum*, *Echeveria*, and *Rochea* have this in common, that in all cases the need of materials for the construction of the young plants is met



by the succulent leaf for some time after its severance from the stem, so that it is not necessary to place the leaf in communication with damp earth with a view to its deriving the requisite water therefrom. They are thus exempted from conditions to which the greater number of plants propagated by gardeners by means of so-called leaf-cuttings are subject.

This method of propagation by leaf-cuttings has long been recognized, and has been particularly applied to Citron and Orange trees, as also to the Wax



Fig. 200.—Formation of Buds on Fronds and Foliage-leaves:

1, 2 on the pinnules of *Asplenium bulbiferum*; 3 on the margins of the lobes of the leaves of *Bryophyllum calicinum*; 4 on the foliage-leaves of *Cardamine pratensis*; 5 on the margin of foliage-leaves of *Malaxis paludosa*. 6 Two buds on the margin of a leaf of *Malaxis paludosa*. 1, 3, 4, 5 natural size; 2  $\times 2$ ; 6  $\times 20$ .

Flower (*Hoya carnosa*), to *Theophrasta Jussieu*, a plant belonging to the Myrsineæ, to the Aucuba Laurel (*Aucuba Japonica*), to the beautiful *Clianthus puniceus*, and to various other plants besides. But it is only quite recently that it has been practised on a vast scale, since the discovery that the Begonias, introduced from the tropical parts of America and now so fashionable as ornamental foliage-plants, and the Gesneraceæ from Brazil with their splendid flowers, are capable of being propagated with extreme facility and in immense numbers by means of their leaves. The cultivator has only to pick one of the foliage-leaves and place it in contact with moist sand or sandy soil, and in a short time

young plants sprout from the leaf and may be transplanted as independent growths. We will briefly describe what takes place.

The first change observed in a leaf which has been cut off for the purpose of forming cuttings is the desiccation of the cells lying next the cut surface. Beneath the layer of dried-up cells a cork-tissue is formed, whilst the dead, outer layer is converted into a bark. A parenchymatous tissue is next formed from the part beneath the cut which is still living; indeed, it is the epidermal cells nearest to the dead layer of cells that initiate this formation of tissue. They grow in a radial direction, elongating and dividing by means of the insertion of transverse walls, the result being a uniform thickening coextensive with the surface of the wound. A little later some of the living cells in the middle of the cut, which are still covered over by the dead layer, begin to divide; and as the tissue there grows in size, it tears the overlying dried layer into shreds and pushes it off in parts. This exuberant tissue has received the name of callus. Whilst the formation of callus is proceeding, suckers are developed at the points of contact of the leaf-cutting with the sand, their numbers being particularly abundant along the projecting ribs of the leaf. In form and function these suckers are entirely similar to the absorbent cells lying close to the growing extremities of roots, and called root-hairs. They are of the greatest importance to the leaf-cuttings in their subsequent processes of development. So long as the leaf adhered to the axis it was supplied with a sufficient quantity of water from that which was ascending through the stem; the aqueous vapour lost through evaporation was replaced by moisture absorbed by the roots from the damp soil and afterwards conducted through the stem to the leaf in question. But when the leaf has been cut off it is no longer able to derive any material from the earth through the intervention of the stem, and as its ordinary epidermal cells have not the power of taking up from the damp soil, which serves as substratum to the leaf-cutting, as much water as is lost by evaporation, the cutting is exposed to the risk of desiccation in spite of its being in contact with a wet substratum. In order to escape this danger and save itself from destruction the leaf treated as a cutting furnishes itself with absorbent cells. By their instrumentality the water, which is particularly needful for the formation of callus, is put by. Even if the materials necessary for the construction of the cells of the callus may be present in abundance in the cells of the leaf, it is of little avail unless these materials are diluted and conducted to the places where they are used up, and for this a much greater quantity of water is requisite than could be retained by the severed leaf. When the callus has reached a certain size numerous roots make their appearance. They usually take their rise from cells of the parenchyma adjacent to a vascular bundle of the leaf, break through the callus, and grow rapidly in length. Only after the development of these roots, which absorb liquid copiously from the substratum by means of their suction-cells, are buds produced on the upper—less frequently also on the under—surface of the leaf-cutting. In *Begonias* it is chiefly cells of the epidermis

that give rise to buds; in other plants, particularly in the Gesneraceæ, in the species of *Peperomia*, a genus belonging to the Pepper order, in *Tournefortia*, *Citrus*, &c., it is cells of the callus that divide and become the rudiments of buds, and indirectly of shoots. In the case of Begonias isolated buds occasionally spring from the callus in addition to the others, but this is not inconsistent with the fact that in these plants the epidermal cells are the favourite places of inception. Especially are those epidermal cells preferred which are situated above the bifurcation of a vascular bundle in the lamina. If an entirely uninjured leaf is laid upon moist sand, the buds develop just above the base of the lamina where the strands radiate out from one another. It is a common custom of gardeners, however, when making use of Begonia-leaves to propagate the plant, to set the petiole in wet sand and to make a number of transverse cuts across the larger veins of the lamina, which is laid flat upon the sand. After this operation quite a host of buds—i.e. new plants—take their rise all along the course of the intersected vein, some immediately in front of the cut, which is covered by a callus, but frequently others again at a distance from that spot. From this we may conclude that the new formation depends principally upon the conduction of material by the veins. No doubt its relative position with regard to the roots developed from the callus to the stock of reserve materials and so forth, also play an important part. The upshot is, however, that numberless cells of the epidermis of the leaf become the seats of inception of new plants, and that buds are able likewise to develop from deeper-lying cells of the callus. Whether the development of an epiphyllous bud has begun in one place or another, there is always in the inceptive area a concomitant production of vascular bundles, which establish a connection between the axis of the bud in process of formation and the previously-developed roots; and it is not long before the axis produces green foliage-leaves capable of assimilating in the presence of light. The leaf-cutting, upon which a miniature plant is now seated, in most cases retains its vitality for a considerable time longer, but at length it begins to turn yellow and gradually it dies. Only that part which produced the buds and roots persists in the form of a pad, forming in some species, for example, in Begonias, a thick, fleshy, cellular body, looking almost like a little tuber.

The phenomenon above described as ensuing in consequence of artificial manipulations takes place sometimes spontaneously in nature in a few plants, and that without the leaf concerned in the process being separated from the axis. Examples of plants which have been observed to bear occasional epiphyllous buds when growing wild in their natural habitats are Cruciferæ (*Cardamine pratensis*, *Nasturtium officinale*, *Roripa palustris*, *Brassica oleracea*, *Arabis pumila*), Papaveraceæ (*Chelidonium majus*), Water-lilies (*Nymphæa guianensis*), Gesneraceæ (*Episcia bicolor*, *Chirita sinensis*), Lentibulariæ (*Pinguicula Backeri*), Aroideæ (*Atherurus ternatus*), Orchidaceæ (*Malaxis monophyllos* and *M. paludosa*), Liliaceæ (*Fritillaria*, *Ornithogalum*, *Allium*, *Gagea*, *Hyacinthus*) and Amaryllideæ



(*Curculigo*). In many cases the buds which arise in the form of little papillæ grow straightway into miniature plants, as in the case of the Cuckoo-flower (*Cardamine pratensis*, see fig. 200<sup>4</sup>), or else little bulbs are formed in the first instance, as in the various species of Garlic and in the Crown-imperial (*Allium* and *Fritillaria*), or small tubers, as in the above specified instances of the genus *Malaxis*. In the one case cells situated in the middle of the lamina—usually above the point of bifurcation of a vascular bundle—are the seat of origin of buds, as, for example, in the Cuckoo-flower, already so often referred to; in other cases, such as *Curculigo*, the buds spring from the extremity of the midrib. The little orchid *Malaxis paludosa* (see fig. 200<sup>5</sup>), which is a native of moorlands in North-western Europe, develops its diminutive buds principally on the surface and margins of the upper portions of the green foliage-leaves, and these buds appear in such large numbers that several botanists state in their descriptions that the leaves of *Malaxis paludosa* are for the most part “shortly ciliated”. Of all the manifold kinds of epiphyllous leaves these little structures produced on the green leaves of the Orchid in question possess a surpassing interest on account of their form. Each bud (two of which are shown in fig. 200<sup>6</sup>) consists of a yellowish-green cellular body, shaped like a kernel, and of a layer of cells hanging loosely together and enveloping the kernel like a sac. At the free extremity the cells of the envelope form a kind of ring, which constitutes the rim of a round depression. The resemblance of these buds to the seeds of Orchids, especially to those of *Malaxis paludosa*, is obvious on the most cursory examination, and it will again be referred to in a subsequent section.

Buds are found much less frequently on scale-leaves and floral-leaves than on the green foliage-leaves. Sometimes they may be observed to spring from bulb-scales if the latter are stripped off the axis and put into moist sand. In these cases they are invariably developed at the spots where the scales have been cut and injured. Dutch cultivators of bulbs make use of this property to propagate hyacinths direct from the bulb-scales. They cut out the axis of the bulb, remove also any rudiments of floral axis which may be present, and cut transversely through the lower part of the bulb-scales. Not infrequently the bulb-scales are also partially divided longitudinally. One would think that after such treatment the bulb must sooner or later perish; but, on the contrary, a crowd of small bulb-like buds are produced on the scales at the edges of the cuts, and cases are known of over a hundred young bulbs being obtained in the manner described from the scales of a single hyacinth bulb.

Of all epiphyllous buds those originating in the tissue of floral-leaves are, as stated, the least common. Minute buds have, however, been repeatedly observed to be developed, instead of seeds, on the carpels in the interior of the fruits of several species of *Crinum* and *Amaryllis*. They were seated on round bodies of tissue, which were not distinguishable from little tubers. When laid on damp soil, each produced a new plant. We need only allude here to the cases of parthenogenesis, which will be discussed later on, wherein seeds capable of

germinating are developed without fertilization from the ovules concealed in the ovary.

The instances of bud-formation above enumerated, when considered with respect to their origin, show that not only cells of roots, but also those of all regions of the stem, and of scale-, foliage- and floral-leaves may become initial cells of buds, or, in other words, of rudimentary shoots. Hence we may draw the conclusion that all the living protoplasts which are capable of division in whatever part of the plant their cells are situated, from the root-tip to the highest apex of the stem, and from the scale-leaves to the ultimate floral-leaves, have the power of undertaking the function of renovation without previously undergoing fertilization. Under ordinary circumstances, no doubt, it is only protoplasts in the cells of the axis, close to the spots where the foliage-leaves emerge, which turn into rudiments of shoots, and the most natural explanation of the selection of these places is that the constructive materials prepared or temporarily deposited in the foliage-leaves may there be turned to account at first hand; but in extraordinary circumstances—*i.e.* as a consequence of unfavourable climatic conditions, or of dangerous injuries, and particularly under the influence of approaching peril of death—the important task of initiating new plants devolves also upon cells situated at most widely different parts of the parent stock, cells which otherwise would certainly not have assumed this function. In these cases it is astonishing to see how stress of external circumstances results in an entirely new division of labour in the cells of the tissue affected thereby; how in one place a protoplast, originally destined to play an altogether different part, divides and becomes the starting-point of a fresh plant, whilst the protoplasts of neighbouring cells convey constructive materials to that particular member of their fraternity and are regularly consumed by it. Very different would have been the order of things and the kind of co-operation of adjoining protoplasts under ordinary conditions!

---

## 2. REPRODUCTION BY MEANS OF FRUITS.

Definition and Classification of Fruits.—Fertilization and Fruit-formation in Cryptogams.—The Commencement of the Phanerogamic Fruit.—Stamens.—Pollen.—Arrangements for the Protection of the Pollen.—Dispersion of Pollen by the Wind.—Dispersion of Pollen by Animals.—Allurements of Animals with a view to the Dispersion of Pollen.—The Colours of Flowers considered as a means of attracting Animals.—The Scent of Flowers considered as a means of attracting Animals.—Opening of the Passage to the Interior of the Flower.—Reception of flower-seeking Animals at the entrance to the Flower.—Taking up the Pollen.—Dispersion of the Pollen.—Cross-pollination.—Autogamy.—Fertilization and Fruit-formation in Phanerogams.

### DEFINITION AND CLASSIFICATION OF FRUITS.

To all appearance there is no difference between the protoplasts which develop into brood-bodies and those which are the points of origin of fruits. Nevertheless, it has been ascertained by experience that the protoplast, which is the starting-point of a brood-body, evolves its constructive energy without receiving any special stimulus from the protoplasm of a second cell of distinct origin, whereas for the development of a fruit the necessity of such a stimulus is a characteristic and distinctive feature of the phenomenon. Brood-bodies may spring from any part of a plant. If the parent-stock as an individual is in danger of perishing, brood-bodies are developed from protoplasts which otherwise would never have been called upon to play such a part. Brood-bodies may develop on roots, stems, and leaves, on foliaceous prothallia, and on hyphal filaments. They may be formed above or below the ground, and upon or beneath the surface of water. Their origin may be from superficial cells or from cells deeply seated in a tissue. It is scarcely going too far to say that in cell-aggregates of large dimensions the protoplasm of every young cell is potentially the starting-point of a brood-body.

If a fruit is to arise, the *ooplasm*, *i.e.* the protoplasm destined to initiate a new generation, must unite with the fertilizing protoplasm, which is called *spermatoplasm*. The two protoplasts concerned in this phenomenon originate at separate spots, and if they are to coalesce the space between them must be surmounted. One at least of the two protoplasts must accomplish a change of place, and this locomotion must take place in a definite direction. The union of two protoplasts which have been formed at places separated in space from one another constitutes the essence of the process of fertilization, and it results in a change in the ooplasm which, in accordance with our idea of the minute structure of the substances in question, may be looked upon as a displacement of molecules and an alteration in their grouping. Sometimes this internal rearrangement is plainly manifested externally by a change of form and colour, or by an increase in size; and where this occurs it ensues immediately upon fertilization. But for the most part no alteration in the fertilized ooplasm is perceptible at first, and it would be difficult to specify any certain signs whereby the fertilized ooplasm may be distinguished from the unfertilized. It is, however, known by experience that in most cases



the unfertilized ooplasm dies without developing further, whereas the fertilized ooplasm, after a longer or shorter period of rest, exhibits a characteristic growth and becomes the point of origin of a young organism, the new generation. The ooplasm rendered capable, by fertilization, of this particular kind of growth is to be considered as an *embryo*, even in cases where no outwardly-visible change in form, size, or colour has taken place.

Both ooplasm and spermatoplasm are formed in special cells at definite spots on a plant which is preparing to reproduce itself by means of fertilization. The cell-chamber wherein the ooplasm is developed, and which is itself adapted to the reception of foreign matter, and constitutes the point of origin of the embryo, will in future be called an *oogonium* ( $\psi\omicron\nu$ =egg;  $\gamma\beta\upsilon\omicron\varsigma$ =parentage); the cell wherein the spermatoplasm is brought to the proper form and composition for the purpose of fertilization is called an *antheridium* in the case of a Cryptogam, and a *pollen-grain* in the case of a Phanerogam. In a few instances the ooplasm is set free from the oogonium and fertilized outside it; the oogonium has then, of course, nothing more to do with the subsequent processes of development. In other cases fertilization takes place within the oogonium; the oogonium persists in a more or less altered form as the immediate envelope of the embryo, and is then designated by the name of "carpium" ( $\kappa\alpha\rho\iota\omicron\varsigma$ =fruit), or briefly "carp". In yet other instances it is possible, at the very earliest stages of development, to distinguish a special multicellular envelope surrounding the oogonium. To this envelope we may apply the term "amphigonium" in order to simplify the terminology. If the amphigonium is later on converted into the coat of the carpium, it may be called an "amphicarpium". In many plants this envelope to the oogonium is succeeded externally by a second called a "pericarpium", which will be the subject of more detailed study later on.

Now what ought we to take to be the fruit? To try to conform to ordinary usage, or to adopt the terms employed in other sciences, would cause fatal confusion. The most expedient course, therefore, seems to be to put aside the names and definitions adopted in other departments and to lay down an independent and unambiguous definition of the plant-fruit, and apply it to all plants. Thus, from the botanical point of view, *we consider every structure to be a fruit which is the product of fertilization, and at the same time constitutes the first step towards the renewal of the fertilized plant.* This definition includes the ooplasm, which is fertilized outside the oogonial envelope, and forms the starting-point of a new individual; there may, therefore, be fruits each consisting of nothing more than an embryo. But usually the ooplasm is enveloped by a coat, which may be single or double, or even threefold. Fertilization then takes place within these coverings, and the influence of the spermatoplasm extends more or less beyond the ooplasm to its investments. In such cases the coats also are involved in the process of fruit-formation. They are stimulated to grow in a particular manner and take the form of a mantle clothing the embryo, of a protective cover, or of some contrivance which promotes the further development of the embryo and its full

expansion into a new generation. Fruits of this kind have sometimes a very complicated structure. In them we are able to distinguish a complex outer coat, and within, the embryo with its tightly adherent covering, the latter portion of the fruit being that which has from ancient times borne the name of *seed*. Fruits thus come before us as a series of forms, of which the members at opposite extremities of the series differ greatly, but are linked together by a large number of intermediate forms. At one end of the chain we have the unicellular fruits of the microscopic Desmids, at the other the fruits of the Coconut, which is differentiated into seeds on the one hand and several envelopes on the other, and is as large as a man's head.

As already stated, the spermatoplasm acquires the composition and form whereon its fertilizing power depends within the confines of certain special cells. Extreme variety is, however, found to prevail in this connection. In some plants, especially those which conduct the process of fertilization under water, the spermatoplasm takes the form of minute particles usually furnished with special motile cilia to enable them to swim about. These have received the name of *spermatozoids*. They escape from the cell-chambers in which they were formed into the water, rush about for a short time or are carried by currents in the water, and finally reach the ooplasm, whereupon they place themselves in contact with it, and enter into combination with it in a manner which may best be likened to the merging together of two drops of oil floating upon the surface of water. In another category of plants the spermatoplasm does not escape from the cell in which it has been developed, but this cell itself enters into combination with the oogonium as a whole, and a possibility is afforded in a variety of ways for the two kinds of protoplasm to coalesce within a single enveloping cell-membrane. A third category of plants is remarkable for the fact that the spermatoplasm does not coalesce as a whole with the ooplasm, only a portion of it passing to the ooplasm.

The above prefatory remarks give some idea of the extreme variety which exists in the processes of fertilization, and it is no easy matter to give a short and concise, and at the same time accurate, presentation of the facts involved, especially if one tries not to use more than is absolutely necessary the innumerable technical terms invented in recent times. Even taking into account only the most important of the phenomena above referred to, we find twelve different processes or types of fertilization and fruit-formation, and it will be the object of the next chapter to present these in order, beginning with the simplest cases and concluding with the most complicated.

It will materially conduce to clearness of exposition if, in considering these phenomena, we adhere to the old classification into *Cryptogams* and *Phanerogams*, which was introduced by Linnæus. According to the etymology of the words, *Cryptogams* are plants which are fertilized secretly, whilst in *Phanerogams* the process of fertilization is apparent. Since the microscope has been perfected and brought into common use this distinction has no doubt lost its significance. If, however, we adopt a somewhat different interpretation of these terms, we may

continue to use them with advantage. Thus, under the name of Cryptogam we shall include all plants destitute of flowers in the ordinary sense and possessing organs of fructification which are not clearly visible excepting under the microscope; whilst the term Phanerogam will comprise such plants as bear flowers, and have organs of fructification which are visible without aid from the microscope and are of the nature of metamorphosed leaves. The retention of these old and familiar terms is rendered all the more desirable by the fact that another important distinction, which is inherent in the process of fertilization itself, and has not as yet received sufficient attention, is involved in the separation of Cryptogams and Phanerogams, namely, that in Cryptogams fertilization takes place in water or in a watery medium, whereas the process in Phanerogams is accomplished almost exclusively in the air.

### FERTILIZATION AND FRUIT-FORMATION IN CRYPTOGAMS.

In the mountain districts of Central Europe, after the winter snow has melted and the turbid water derived from it has gradually cleared itself up, a beautiful sight is afforded, especially when a ray of sunshine strikes the water, by the dense crowds of short delicate filaments of a bright emerald-green colour, which everywhere form a coating to the stones at the bottom of streams and to the sides of the troughs used to convey spring-water from the heights. These green threads belong to a plant named *Ulothrix*. Each separate filament consists of numerous cells joined together so as to form a chain, as is shown in fig. 201<sup>1</sup>. When these filaments are mature, and the time has come for the production of fruit, the protoplasmic contents of the separate cells break up into a number of spherical green masses, which, however, continue to be held together in a rounded cluster by means of a colourless substance. An aperture is now formed in the wall of each of the cells in question, and through this opening the conglomerate mass escapes into the surrounding water (see figs. 201<sup>2</sup> and 201<sup>3</sup>). The individual masses of protoplasm which compose the conglomerate are set free shortly afterwards, and each exhibits at its anterior extremity a pair of revolving cilia, by means of which it swims about in the water (fig. 201<sup>4</sup>). When in the course of their peregrinations two protoplasts which originated in one and the same cell-cavity encounter one another they get out of each other's way; if, on the other hand, the protoplasts from cells belonging to different filaments meet, far from avoiding one another, they come into full collision with their anterior ciliated extremities, turn over, and lay themselves side by side and coalesce, forming a single body with four cilia (see fig. 201<sup>5</sup>). A little later the cilia vanish, and the product of the coalescence comes to rest. This fusion is the simplest conceivable case of fertilization in the whole realm of plants. The product of fertilization is the fruit. It consists in *Ulothrix* of the little lump of protoplasm formed by the process of coalescence just described, which now surrounds itself with a thick cell-membrane, and fastens on to some stationary body under water (see fig. 201<sup>6</sup>). We have nothing to do at present with the subsequent development of this fruit; it is



sufficient to remark in order to explain the illustration that the attached unicellular fruit does not produce again immediately a string of cells, but that first of all swarmspores are developed from its protoplasm (see figs. 201<sup>7</sup> and 201<sup>10</sup>), and these fasten on to appropriate spots, inclose themselves in cell membranes, divide and ultimately initiate new filaments composed of cells arranged in linear series as before.

In *Ulothrix* and allied genera the protoplasts which pair as a first step to the formation of fruit do not differ from one another in form, size, colour, or mode of locomotion, and it would be impossible to determine from outward appearances which of them acts as fertilizer and which is fertilized. The terms *ooplast* and

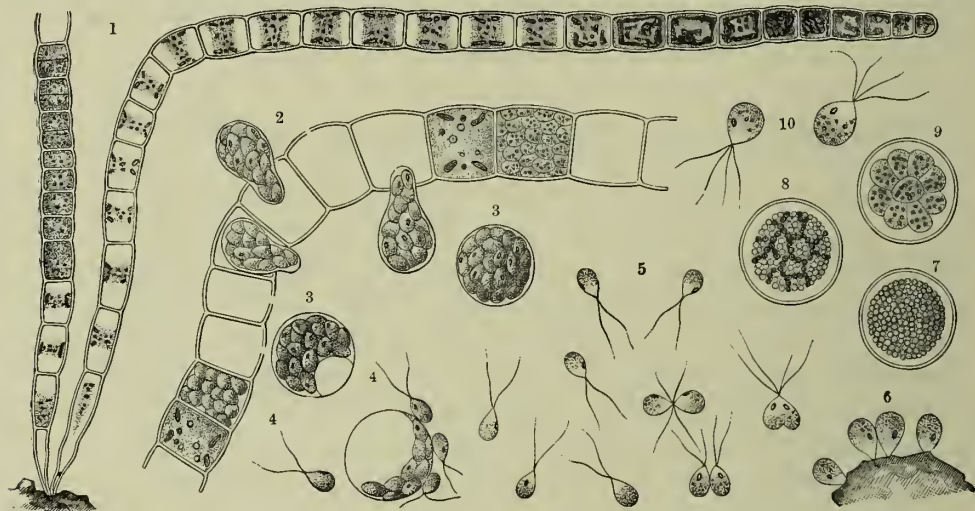


Fig. 201.—Fertilization and fruit-formation in *Ulothrix zonata* (partly after Dodel-Port).

<sup>1</sup> Two filaments composed of cells joined together in chains. <sup>2</sup> Escape of conglomerated gametes. <sup>3</sup> Spherical conglomerate of gametes after it has escaped. <sup>4</sup> Separation of the gametes. <sup>5</sup> Gametes swimming about and pairing. <sup>6</sup> Fruits (products of the pairing of gametes) attached to a substratum. <sup>7-9</sup> Subsequent development of fruit. <sup>10</sup> Two swarmspores produced by fruit. <sup>1</sup>  $\times 250$ ; <sup>2-10</sup>  $\times 400$ .

*spermatoplast* are therefore not applied to them, but they are called *gametes*, and the entire process described in connection with them may be spoken of as *fruit-formation by pairing of gametes*. This process of pairing is, so far as it can be apprehended by our senses, a mutual permeation of the two protoplasmic bodies, and we may suppose that a rearrangement of molecules is caused thereby, which endows the product of pairing with the power of developing independently. This assumption is supported in particular by the fact that if any gametes, after being set free from the conglomerate, fail to pair they undergo no subsequent development but deliquesce in the surrounding water and perish.

The Wracks or Fucaceæ, which grow profusely in the sea, resemble *Ulothrix* inasmuch as the protoplasts, destined to act as fertilizers, escape from their cell-cavities, fertilization consisting of a fusion of free protoplasts disconnected from the mother-plant. But these Wracks differ very strikingly from *Ulothrix* and allied forms in that the protoplasts are of two kinds, there being an obvious diversity in

size and form between ooplasts and spermatoplasts. The thallus in all species of *Fucus* is tough and leathery, brown in colour, foliaceous, and dichotomously branched or lobed, and has interspersed here and there air-containing swellings which serve as floats. The apices of the lobes are punctate, and each spot corresponds to an internal cavity which has the form of a globular pit (see fig. 202<sup>1</sup>). Sections through these cavities show that a large number of segmented filaments known as "paraphyses" spring from the lining-layer of the cavity. In *Fucus vesiculosus* (figs. 202 and 203) these filaments remain concealed in the cavity; in some other species of *Fucus* they protrude through the narrow orifice (ostiole) of the cavity in the form of a pencil of hairs. Amongst the filaments other structures are also formed within the cavity. A few of the cells lining the cavity swell into papillæ, and each becomes divided by the intercalation of a transverse septum

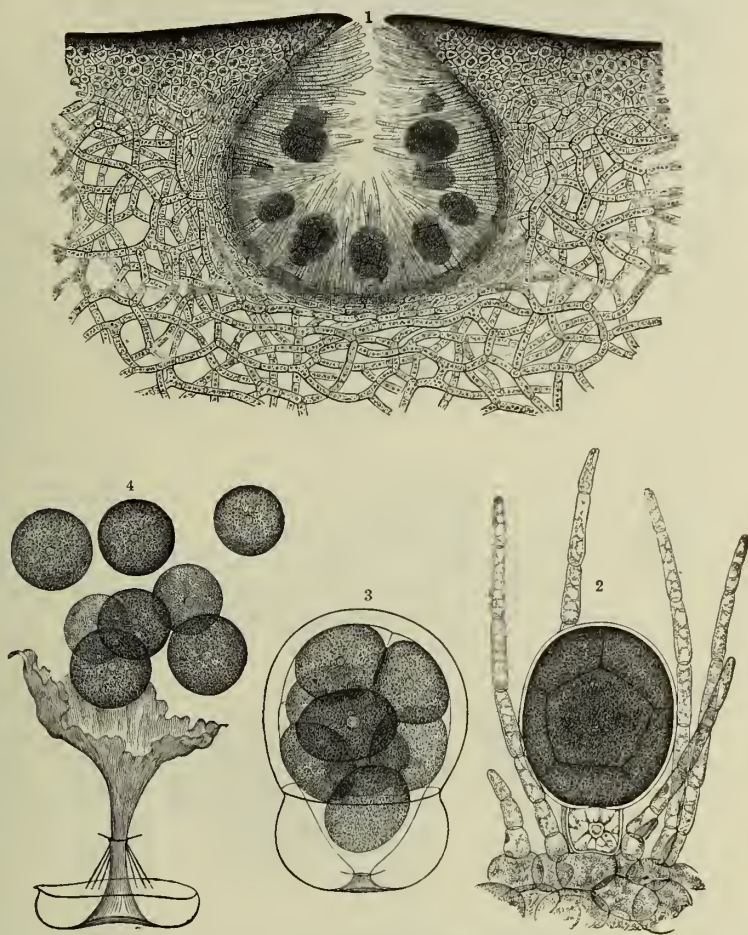


Fig. 202.—*Fucus vesiculosus*.

- <sup>1</sup> Longitudinal section through one of the cavities in the thallus. <sup>2</sup> A vesicle surrounded by paraphyses from the bottom of the cavity. <sup>3</sup> A detached vesicle containing eight ooplasts; the inner lamella swollen up. <sup>4</sup> Liberation of the ooplasts from a rent vesicle. (After Thuret.)

into two cells, one of which is spherical, whilst the other assumes the form of a stalk bearing the upper one (see fig. 202<sup>2</sup>). The protoplasm in the spherical cell is dark brown, and breaks up into eight parts, which round themselves off and constitute the ooplasts. The thick wall of the spherical cell resolves itself into two layers, of which the inner one incloses the eight rounded protoplasmic bodies like a bladder. This bladder stuffed full of ooplasts next detaches itself entirely, and glides upward between the paraphyses until it reaches the orifice of the cavity.



Here the bladder splits into two lamellæ, and finally the inner lamella becomes inflated, bursts and shrivels up, leaving the eight ooplasts free (see figs. 202<sup>3</sup> and 202<sup>4</sup>).

Whilst a certain proportion of the individual plants of *Fucus vesiculosus* develop ooplasts in the cavities in their lobes, other individuals give rise to spermatozooids

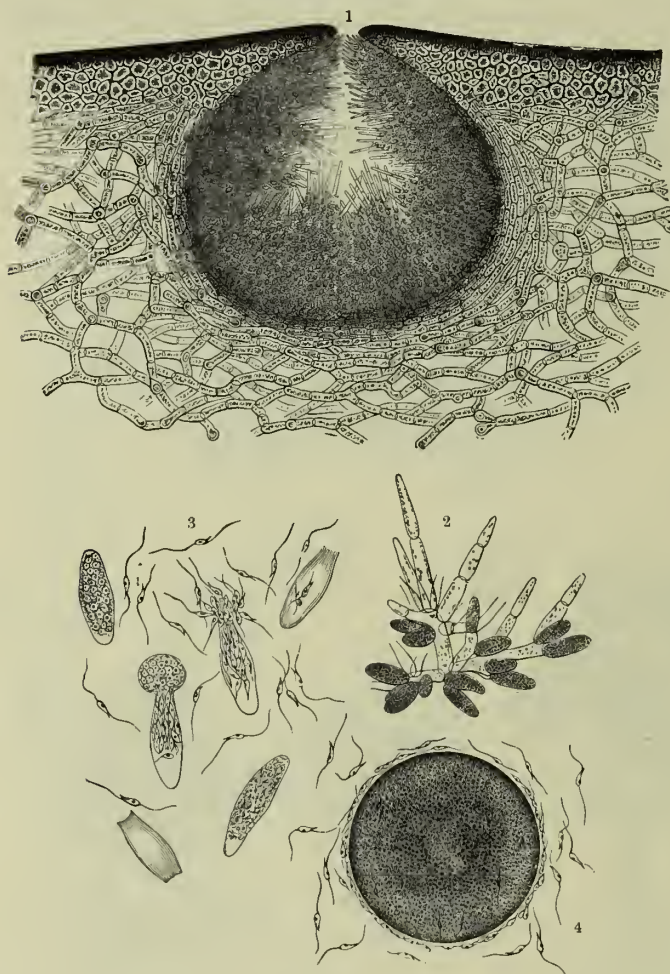


Fig. 203.—*Fucus vesiculosus*.

<sup>1</sup> Longitudinal section through a portion of a thallus including a cavity full of antheridia. <sup>2</sup> Antheridia extracted from a cavity of the kind. <sup>3</sup> Spermatozooids escaping from the antheridia. <sup>4</sup> Spherical ooplast covered with spermatozooids. 1×50; 2×160; 3, 4×350. (After Thuret.)

in similar cavities (see fig. 203<sup>1</sup>). The cells lining the hollows develop papillose protuberances which grow longitudinally, divide and form a ramifying mass of cells as is shown in fig. 203<sup>2</sup>. Here and there the extremities of branches in this mass of cells have a dark brown colour, and their protoplasmic contents are broken up into a number of minute portions (the spermatozooids). These vesicles become detached and collect at the orifice of the cavity. This happens especially at the time when that zone of the sea-shore where the wrack grows is left dry, and the *Fucus* plants are lying flat upon the stones, and look like brown and faded leaves. At the recurrence of high-tide, when the wracks are again submerged, the cells full of spermatozooids

burst, and the tiny spermatozooids formed from their protoplasmic contents swarm out into the surrounding water. Each spermatozoid has a sharp and a blunt end, exhibits a so-called eye-spot, and is furnished with two long cilia by means of which it swims about in the water (see fig. 203<sup>3</sup>). Analogy to similar processes which take place in Mosses makes it seem probable that the ooplasts above described as lying near the orifices of cavities in the thallus secrete some compounds or other—presumably organic acids—which attract the spermatozooids swarming in



the water. The actual fact is that spermatozoids which come into the vicinity of the spherical ooplasts adhere to them in such large numbers that a sphere is sometimes entirely coated with spermatozoids (see fig. 203<sup>4</sup>).

It has also been observed that the spherical ooplasts are set rolling by the adherent spermatozoids, and are thus removed from the places where they previously lay stranded. The fertilizing effect exercised by the spermatozoids, one of



Fig. 204.—Fertilization and Fruit-formation in *Mucorini*, *Siphonaceæ*, and *Floridææ*.

1-4 Conjugation and fruit-formation in *Sporodinia grandis*. 5, 6 *Vaucheria sessilis*. 7 Fruit-rudiment with trichogyne of *Dudresnaya coccinea*. 8 Antheridia of the same plant with spermatozoids in the act of abjunction. 9 Fruit of the same. 1-4  $\times 180$ ; 5, 6  $\times 250$ ; 7, 8  $\times 400$ ; 9  $\times 250$ . (7-9 after Bornet.)

which, as it appears, coalesces with the ooplasts, consists doubtless in a rearrangement of molecules, and the first outwardly visible result of this rearrangement is the envelopment of the ooplast in a tough cell-membrane. The body must now be considered to be a fruit—a unicellular fruit, which remains unaltered in a state of rest for some time, but at length bestirs itself, and stretching out attaches itself firmly to the ground by means of root-like outgrowths. It then divides and gradually develops into a fresh *Fucus* plant.

In the two cases just described, the ooplasts are not fertilized till after they have

escaped from the cells of the mother-plants into the surrounding water, and at the time of fertilization they are destitute of any special coverings of their own. In the plants to be dealt with next, on the other hand, the ooplasts at the time of fertilization are still in connection with the mother-plant. The cell-membrane, which maintains this union, persists as an envelope to the protoplasm which is to undergo fertilization. There are two ways in which a fertilizing protoplast may exercise its influence upon a protoplasmic body thus inclosed in a cell-membrane. Either a piece of the envelope is broken through and a free passage made for the spermatoplasm to the ooplasm, or else, if a true fertilization takes place, it must be by osmosis through the envelope.

The solution and removal of part of the cell-membrane enveloping the ooplast, and the opening up of a passage in which the spermatoplast can unite with the ooplast, is observed to occur in the Mould-fungi known as *Mucorini*, and also in the innumerable little green and brown water-plants which, on account of their characteristic mode of fertilization, have received the name of *Conjugatae*. In these plants the coalescence of the two kinds of protoplasts is always preceded by a process of "conjugation", that is to say, the envelopes surrounding those protoplasts come in contact and grow together, and a special cavity is thereby created in which the fusion of the protoplasts can take place. This method of fertilization is shown in the clearest manner in fig. 204<sup>1,2,3,4</sup>, the instance being that of *Sporodinia grandis*, a Fungus belonging to the *Mucorini*. Two more or less parallel tubular hyphæ put forth lateral protuberances (fig. 204<sup>1</sup>) which stretch out towards one another until their free ends come into contact and cohere. As soon as this union is effected, a transverse wall is formed on either side of the plane of contact, and it is now possible to distinguish in the limb connecting the two hyphæ a median pair of cells supported by the two basal portions of the outgrowths (see fig. 204<sup>2</sup>). The connecting limb is usually likened to a yoke (ζυγόν). The wall arising from the junction of the outgrowths, and now separating the two cells in the middle of the yoke, dissolves, thus producing a single cell-cavity (instead of the two), which is called a "zygogonium". The two protoplasts inhabiting the pair of cells were hitherto separated, one being derived from the hypha to the right, and the other from the hypha to the left; they are two different individuals, but, upon the dissolution of the wall between them, they coalesce within the zygogonium. This coalescence is to be looked upon as the act of fertilization. The membrane of the median cell, which surrounds the blended mass of protoplasm, thickens, and, in the selected instance of *Sporodinia grandis*, becomes warted, whilst in *Mucor Mucedo* (fig. 193<sup>3</sup>) it becomes rough and wrinkled, and in other *Mucorini* even spinose. It also acquires a decided dark coloration. Lastly, the dark median cell detaches itself from the basal portions of the original outgrowths, which have held it up to that time, and thus becomes free and independent (see fig. 204<sup>4</sup>). It then drops just as a cherry does from the twig of a tree, and, like the cherry, it must be designated as a fruit, although it consists of a single cell only. Fruits of this kind have received the name of "zygotes".

It is no more possible to say which of the two protoplasts uniting in the zygogonium of *Sporodinia grandis* is fertilized and which acts as fertilizer, than it is to predicate of the pairing protoplasts of *Ulothrix*, that the one is the ooplast, and the other the spermatoplast. Theoretically we must assume there is a difference, and it probably consists in peculiarities of molecular constitution, but no perceptible difference can be detected in size, configuration, or colour, nor is there any apparent distinction in respect of origin.

In the *Desmidiaceæ* also, of which two examples (*Closterium* and *Penium*) are given in vol. i. Plate I. figs. *i* and *k*, and in the *Diatomaceæ*, whose species are reckoned by hundreds, no perceptible external difference exists between the protoplasts which unite for the purpose of fertilization. Only in the *Zygnæmaceæ* is it possible to look upon a particular one of the combining protoplasts as an ooplast, and the other as a spermatoplast, and the distinction is in this case founded on their relative positions. An instance of the mode of fertilization prevailing in these plants is shown in Plate I. fig. *l*, in the first volume, the case chosen for illustration being that of *Spirogyra arcta*, which consists of green filaments of a slimy consistence, and occurs very commonly in our ponds. The cells are arranged in linear series, and from some of them are formed lateral outgrowths like those produced by the tubular cells of *Sporodinia grandis*. As in *Sporodinia*, the outgrowths from opposite cells come into contact, coalesce, and form a kind of yoke. Usually a number of the opposite cells of two filaments floating close together in the water establish connecting links of the kind, which resemble the rungs of a ladder (see vol. i. Plate I. fig. *l*, to the right). The wall formed by the coalescence of the two apices of the outgrowths is removed by solution, and a channel connecting the opposite cell-chambers of the *Spirogyra*-filaments is thus opened up. In the meantime the protoplasm in each of these cells undergoes a change. Hitherto it has been occupied by a chlorophyll-body in the form of a spiral band, but now it assumes the form of a dark-green spheroidal mass, which is destined to unite with the one opposite to it. In *Spirogyra* this coalescence does not take place in the middle of the connecting canal as in *Mucor* and *Sporodinia*, but the green ball of protoplasm from one cell glides through the transverse passage into the opposite cell-chamber, and there coalesces with the second protoplasmic mass which has remained at rest and not changed its position. It is permissible to call the resting protoplast an ooplast, and the one which moves across to it a spermatoplast; but it must again be expressly stated that in *Spirogyra* no difference in size, shape, or colour can be detected between the two uniting protoplasts. It is worthy of note that the zygote produced by the coalescence, and now assuming an ellipsoidal shape, is not equivalent in bulk to the two protoplasts, as one might expect, but that its volume is obviously smaller. We may infer from this that at the moment of coalescence a fundamental change in the molecular structure of the entire mass takes place. The characteristic property of fertilization in the *Conjugatæ*—of which *Sporodinia grandis* and *Spirogyra arcta* have here been chosen as examples—consists in the union of two separate individuals by means of the



formation of a yoke between opposite cells which put forth lateral outgrowths towards one another for the purpose; this is the reason why this kind of fertilization is called conjugation, and the plants concerned are named *Conjugatae*.

Similar to conjugation, but differing from it in several essential particulars, is the mode of fertilization by means of a protruding outgrowth from the antheridium, which pierces through the wall of the oogonium. This method is observed to occur in particular in the destructive parasites comprised under the name of Peronosporæ. The species named *Peronospora viticola*, which is represented in fig. 205, has attained a melancholy notoriety as a parasite on the Vine, and to the same group belong *Peronospora infestans*, which causes the Potato-disease, *Cystopus candidus*, known as a deadly parasite on Cruciferous plants, the various species of *Pythium*, &c. Tubular hyphæ develop directly from the spores of these Peronosporæ, which attack the fresh foliage, green shoots, or young fruits of the particular flowering plants that they select to serve as hosts. The hyphæ bore into the green tissue, piercing through the cell-walls and growing in the intercellular spaces, where they ramify extensively. Segmentation of the hyphæ by the introduction of partition-walls is comparatively rare, but very frequently little suckers, called "haustoria", are sunk into the interior of the living cells of the host (see vol. i. p. 165, fig. 32<sup>1</sup>). These hyphæ infesting the green tissues of the host-plant swell up at their blind extremities into globular heads, and a septum is introduced in each case to partition off the terminal sphere from the rest of the tube, which preserves its cylindrical form. The spherical cell is an oogonium, and the protoplasm forming its contents is the ooplasm. The latter differentiates itself into two portions, namely, a central darker ball and a clearer transparent enveloping mass. The antheridia containing the spermatoplasm develop in the form of lateral clavate outgrowths from another tube, or more rarely from the same tube. These protuberances grow towards the oogonium and apply themselves to its surface. As soon as the antheridium touches the oogonium it sends out from the point of contact a conical or cylindrical hollow process which pierces the wall of the oogonium and penetrates to the dark ball in the middle of the ooplasm (see fig. 205<sup>3</sup>). Meanwhile the protoplasm in the antheridium has differentiated itself into a parietal lining on the one hand and the true spermatoplasm on the other. The antheridial process, which has received the name of "fertilizing-tube", opens at the extremity buried in the interior of the oogonium; within an hour or two the spermatoplasm has flowed through this channel to the ooplasm and become so completely merged with it that it is no longer possible to recognize any boundary between the two. A short time afterwards the fertilized ooplasm incloses itself in a thick cell-membrane composed of several layers. The outermost layer is usually rough and warty, and in some species is even beset with spikes. The fruit thus formed is unicellular and remains so. It frees itself from the now decaying oogonium—thus effecting its separation from the mother-plant—and then enters upon a long period of rest. The new generation developed from the fruit begins as a tube

which subsequently, in some cases, puts out sac-like processes and branches and fashions itself into the likeness of the mother-plant without passing through any intermediate stage; or in others, the tube, which represents the embryo, produces first of all from its protoplasm a number of swarmspores. These roam about for a period and then seek out a convenient spot where they come to rest and develop into new individual plants. The additional production by *Peronospora* of spores on dendritically-branched hyphæ growing out through the



Fig. 205.—Fertilization, fruit-formation, and spore-formation in the *Peronosporæ*.

<sup>1</sup> A bunch of grapes attacked by the Vine-Mildew. <sup>2</sup> Spores on branched stalks projecting through a stoma of a Vine-leaf

<sup>3</sup> Fertilization in *Peronospora viticola*. <sup>4</sup> A single spore. <sup>5</sup> A single spore the contents of which are dividing into swarm-spores. <sup>6</sup> A single swarmspore. <sup>1</sup> natural size; <sup>2</sup>  $\times 80$ ; <sup>3-5</sup>  $\times 350$ ; <sup>6</sup>  $\times 380$ . (<sup>3-6</sup> after De Bary.)

stomata of the green host-plants is shown in fig. 205<sup>2</sup>, but an opportunity will occur later on of discussing the details of that process.

The Siphonaceæ exhibit a different mode of fertilization from those processes which involve the preliminary construction of a fertilization-tube and a conjugation-canal respectively. All the Siphonaceæ live in water or on damp, periodically submerged earth; they contain chlorophyll and are neither parasites nor saprophytes. We may take as a type of this group of plants, which includes forms of great diversity, a species of the genus *Vaucheria* (see vol. i. Plate I. fig. a, and text p. 23) and use it also to illustrate the processes about to be considered.



If a green filament of *Vaucheria* is examined under the microscope it is found to consist of a single tube without septa, but with numerous saccate branches. The sac-like outgrowths serve a variety of purposes; those at the base fasten the tube to the substratum, those at the free extremity develop swarmspores, whilst those springing laterally from the filament have the functions of fertilization and fruit-formation. The lateral outgrowths are of two kinds (see figs. 204<sup>5</sup> and 204<sup>6</sup>). One form is short, thick, and oval, and usually projects obliquely; the other is a slender cylinder curved like a chamois horn or wound round in a spiral, and sometimes it is subdivided into several little horns. The protoplasm in these sacs severs itself from the protoplasm of the main tube and a partition of cellulose is inserted in the plane of disjunction in each case. We have thus corresponding to each protuberant sac a cell-cavity or receptacle which incloses the protoplasm destined to take part in the formation of fruit. The obliquely-oval receptacles contain ooplasm and are oogonia, the curved, cylindrical receptacles inclose spermatoplasm and are antheridia. Their development is accomplished rather rapidly. It usually commences in the evening, and by the following morning the oogonia and antheridia are already completed. During the course of the forenoon an aperture appears at the apex of the oogonium, whilst simultaneously the ooplasm within it contracts into a sphere. The spermatoplasm in the antheridia has meanwhile broken up into a large number of oblong spermatozoids, with a cilium at each end. After this has happened the free extremity of the antheridium bursts open, and the minute spermatozoids are expelled in a swarm into the surrounding water. Some of them reach a neighbouring oogonium, pass through the opened summit into the interior of the receptacle, and there coalesce with the ooplasm which has contracted into a green sphere. In connection with this phenomenon there is the following very striking circumstance to be noted. Where, as is usually the case, an oogonium and an antheridium are developed in close proximity to one another on the same tube, they seldom open simultaneously, and this circumstance most effectively prevents the fertilization of the ooplast by spermatoplasm of the adjacent antheridium; but on the other hand it usually happens that the spermatoplasm from the antheridium of one tube reaches the oogonium of another tube, and in this manner a crossing of the two takes place (figs. 204<sup>5</sup> and 204<sup>6</sup>).

As soon as an ooplast is fertilized it surrounds itself with a tough cell-membrane; the green colour of the protoplasm changes to a dirty red or brown, and the fruit is to be seen imbedded in the oogonium in the shape of a reddish-brown, unicellular sphere. The oogonium dissolves or else breaks off with the fruit inclosed in it. In either case the product of fertilization is removed from the tube whereon it developed and sinks to the bottom, where it undergoes a comparatively long period of rest often lasting through an entire winter. When the unicellular fruit germinates, the outer layer of the cell-membrane splits, and out of the rent emerges a tube of like form to that which produced the fruit.

In every case of cryptogamic fertilization hitherto discussed a union of the



spermatoplasm with the ooplasm occurs. The protoplasts set aside for the purpose of coalescence forsake the cell-interiors when they have attained to maturity, or at least one of the sexual cells liberates its protoplasm so that it reaches the other unfettered and is enabled to effect a union of their two masses. For this result it is necessary for a part of the cell-membrane enveloping the protoplasm in question to be previously removed, for otherwise it would not be possible to effect the kind of union to which the phrase coalescence of protoplasm is properly applicable. On the other hand, many cases exist in which there is no obvious perforation of the wall, although the changes usually following true fertilization take place. Under these circumstances it is difficult to resist the view that if fertilization (*i.e.* a fusion of protoplasts) really happens (as to which difference of opinion still prevails) it is accomplished by means of osmosis. With this qualification we may say that fertilization by means of osmosis is observed in its simplest form in the Erysipheæ, popularly known as Mildews, in the Moulds allied to *Aspergillus* and *Penicillium*, a description of which in relation to their methods of spore-formation is given on pp. 21, 22, and in several Discomycetes, including the curious Fungus named *Ascobolus*, which will be dealt with more thoroughly when we come to the subject of the mechanisms for dispersing spores.

The Mildew occurring on the surfaces of green foliage-leaves appears under the microscope as a peculiar kind of mycelium. The hyphæ, which are filiform, colourless, and densely interwoven, do not penetrate into the intercellular spaces of the tissue of the host-plant, but satisfy themselves with sinking little suckers into the superficial cells of the leaves and stem (see vol. i. p. 165, fig. 32<sup>2</sup>). Here and there these hyphal tubes rise erect from the substratum and abstrict moniliform rows of spores; others put forth short, lateral outgrowths which become partitioned off by the insertion of a transverse wall in each, so that the protoplasm in the outgrowth is shut off from the rest of the protoplasm in the tube. Some of these latter structures are oval or club-shaped, and they contain ooplasm and are to be considered as oogonia; the others are cylindrical and sometimes bent into the form of hooks, and they contain the spermatoplasm and constitute antheridia. In a few species the upper, somewhat swollen end of the outgrowth filled with spermatoplasm—*i.e.* the antheridium—bends over the top of the oogonium and attaches itself closely thereto, without, however, sending any special fertilization-tube into the interior of the oogonium; in other Fungi of the Mildew family both cells—the oogonium as well as the antheridium—are spiral and are coiled round one another, and at the same time pressed tightly together. On the assumption that a true fertilization now occurs, this must, as already indicated, be by a diffusion of the spermatoplasm through the cell-membranes to the ooplasm, causing a change in its ultimate structure which corresponds to fertilization. The ooplasm is thereupon converted into an embryo. The cell inclosing the embryo neither dissolves nor severs itself from the parent-hypha, but divides and becomes differentiated into an upper swollen cell and a lower short,

stalk-like cell, and below the stalk fresh tubular outgrowths develop from the hyphal filament in question which become septate and ultimately form a voluminous multicellular envelope round the embryo.

The now mature fruit preserves its connection with the parent-hypha, and is to be seen seated upon it in the form of a minute sphere. When a large number of fruits are developed simultaneously on the hyphal reticulum—as is the case in *Sphærotheca Castagnei*, which is parasitic on the leaves of Hops—the grey mildew spread over the foliage has the appearance of being studded with the tiny globular heads. From the embryo a new generation is produced. In the species of the genus *Podosphæra* it develops, within the cellular mass just referred to as investing the fruit, into a single tube (*ascus*). The protoplasm within the ascus breaks up and fashions itself into true spores, which abandon the tube and are distributed by the wind. In *Erysiphe*, on the other hand, the embryo becomes septate, and takes the form of a simple or branched chain of cells, and it is not till after this stage that tubes are produced whose protoplasm is transformed into a group of spores. The tubes in question are long, erect, and club-shaped, and they spring from the cells of the aforesaid chain.

The manner of fertilization and fruit-formation in *Penicillium*, and generally in all the forms of Mould which are comprised under the name Aspergillæ, is the same as that described in the case of Mildews (*Erysipheæ*). In them also the extremities of tubular hyphæ which contain the ooplasm and spermatoplasm, respectively, come into close contact. They are either spirally twisted and wound round one another, or else the extremity corresponding to an antheridium is hooked and grasps the other, as is shown in fig. 193<sup>6</sup> (p. 18). Fertilization takes place by osmosis. The embryo produced by the spiral oogonium is septate and multicellular, and develops club-shaped or egg-shaped outgrowths, whose protoplasm breaks up into round or ellipsoidal balls (fig. 193<sup>7</sup>). This structure becomes surrounded by a continuous multicellular tissue, which owes its origin to the upgrowth of a number of hyphæ from the cells at the base of the oogonium. These hyphæ elongate rapidly, ramify, become intertwined, and develop septa until they constitute a spherical envelope round the embryo. The fruit thus constructed is in *Penicillium* about half a millimetre in diameter.

The Floridææ, or Red Seaweeds, are likewise fertilized by means of osmosis. The details of the process are, however, intrinsically different from those observed in Mildews and in the Moulds classed as Aspergillæ. The organs developed for the purpose of fertilization have also quite a different form in Floridææ. Their most striking feature is the so-called “trichogyne”, a long filamentous cell which projects far above the fruit-rudiment. From this structure the characteristic mode of fertilization in Floridææ is called fertilization by aid of a trichogyne. In some Floridææ the cell containing the ooplasm leads directly into the trichogyne; in others the fruit-rudiment which incloses the ooplasm is septate, that is to say, it consists of a row of broad cells which together form a short branch of the ramifying thallus, and adnate to one side of this row of cells is the long, delicate,

filamentous cell called the trichogyne (fig. 204<sup>7</sup>). Rudimentary fruits of this kind are produced on one individual, whilst antheridia are formed upon another. It is much less common for fruit-rudiments and antheridia to be developed on the same individual, and in the few species which do exhibit this combination, self-fertilization is rendered practically impossible by a retardation of the development either of the fruit-rudiments or of the antheridia. The antheridium always takes the form of a limited portion of the thallus, from which separate round cells filled with spermatoplasm are thrown off. Fig. 204<sup>8</sup> represents an antheridial branch of *Dudresnaya coccinea*. A slender branch of the thallus terminates in a group of cells arranged dichotomously, and the outermost of these cells, which become rounded off and detached, contain the spermatoplasm, and must be looked upon as spermatozooids. Unlike the spermatozooids of *Vaucheria* and those of the Characeæ (Stoneworts), Muscineæ, and Ferns, to be described presently, these have no cilia, and do not move by virtue of any power of their own in the surrounding water, but are carried about by currents which are always more or less prevalent at the places where the Florideæ live. Through the action of these currents in the sea, the spermatozooids (or *spermatia* as they are called) reach one of the trichogynes and adhere to it, as is shown in fig. 204<sup>7</sup>. The question as to how far attractive forces emanating from the ooplasm come into play in order to effect this conjunction must remain undecided. It is not impossible that substances may be secreted by the ooplasm and be given off into the environing water, and that they may take part in the phenomenon. Nothing more definite is known beyond the evident fact that the spermatozooids adhere much more commonly to trichogynes than to other objects floating in the neighbourhood. Part of the protoplasm of the adherent cells passes apparently by osmosis into the protoplasm of the trichogyne. The change ensuing upon this process is transmitted to the protoplasm occupying the ventral enlargement at the base of the trichogyne, and in many cases even further to the protoplasm of adjacent cells. Although this propagation of the change in the molecular structure of the protoplasm cannot be directly observed, it may be assumed on various grounds, and we may fairly suppose that the action of the absorbed constituents of the spermatoplasm upon the ooplasm is comparable to that of certain enzymes, which have a convulsive effect upon any protoplasm in their vicinity, and even when they are separated from it by cell-walls cause a displacement and rearrangement of the molecules (see vol. i. p. 464). That the change affecting the protoplasm at a particular spot in the fruit-rudiment is capable of being propagated so long as any protoplasm susceptible of the same change is present, is proved by the fact that it is not the trichogyne itself but the ventral enlargement at its base and the cells adjacent to this enlarged portion which undergo subsequent development. They increase in bulk, whereas the trichogyne shrivels and dies. The cells which contain the protoplasm fertilized through the intervention of the trichogyne must, in my opinion, be looked upon as the fruit. Any subsequent structure arising from them is no longer fruit but a new generation. In Florideæ, as in so many other cases, this new generation preserves its connection with the



mother-plant, but differs conspicuously in form from the generation from which it sprang. This stage having already been dealt with on p. 22, it is here only necessary to mention briefly that the cells of the fruit begin to shoot out after a period of rest of variable duration and abstrict a mass of spores, and that in addition, in most Florideæ, linear series of cells grow from the cells at the base of the fruit, and form a capsular envelope around the young spores.

The Cryptogams that we have still to deal with, viz.: the Characeæ, Muscineæ, and Vascular Cryptogams, differ from those already described in that the oogonium is wrapped up in a special sheath before fertilization takes place, and that the entrance-passage provided for the spermatoplasm is consequently modified in a characteristic manner. This sheath, to which we shall apply the term *amphigonium* (also known as *archegonium*), is in the main of the same construction in all the plants exhibiting it; but as regards the penetration of the spermatozoids into the amphigonium, and the behaviour of the fruit produced from the fruit-rudiment, there are very considerable differences amongst the groups in question. To follow out these diversities in minute detail is not possible within the narrow limits of this book, and I must content myself in the following pages with giving a brief sketch of the most important phenomena.

To begin with the Stoneworts (Characeæ), we find that in them the fruit-rudiment is ellipsoidal in shape, and is borne on a very short unicellular stalk. This stalk is seated upon the so-called "nodal cell", a short discoid cell which forms the pedestal of the large ellipsoidal oogonium, and also gives rise to five tubular cells arranged in a whorl, and twisted spirally round the oogonium, thus enveloping it in a sheath of great beauty (see fig. 206<sup>3</sup>). From the ends of these investing tubes, which project above the oogonium, small cells are separated off, and together constitute a little roof for crown to the amphigonium. Beneath the crown the enveloping tubes are drawn together so as to form a neck which incloses a narrow cavity, and this is the part where at the time of fertilization fissures are formed between the otherwise connate tubes of the envelope, thus enabling the spermatozoids to penetrate into the interior of the amphigonium, and to reach the ellipsoidal oogonium there matured.

The mode of genesis of these spermatozoids is extremely remarkable. They are produced in certain red, globular structures, which are slightly smaller than the fruit-rudiments and have a like origin—that is to say, they take their rise amongst the whorls of lateral offshoots. In some species they are formed on the same individuals as the fruit-rudiments (*cf.* figs. 206<sup>2</sup> and 206<sup>3</sup>), in others the two kinds of structure develop on different individuals, and are thus separated from one another; hence we distinguish Characeæ into monœcious and dioecious species. Each red sphere is composed of eight plates, outwardly slightly convex. Each of these is in the shape of a spherical triangle with indented edges and folds running radially from the centre to the notched margins (see fig. 206<sup>4</sup>). The plates are joined together into a sphere, the notches of the margins fitting into one another so as to form a regular dovetailed suture. From the centre of the gently

concave inner face of each plate a cylindrical or conical cell projects, carrying upon its summit another, capitate, cell. Each of these head-cells is surmounted by long strings of cells, of which the lowest segments are spherical or cylindrical, whilst the rest are short discs (see fig. 206<sup>5</sup>). The whole structure may be likened to a whip with many thongs, and the stalk-cell projecting from the plate has hence been called the "manubrium" or handle. So long as the eight plates of the sphere are

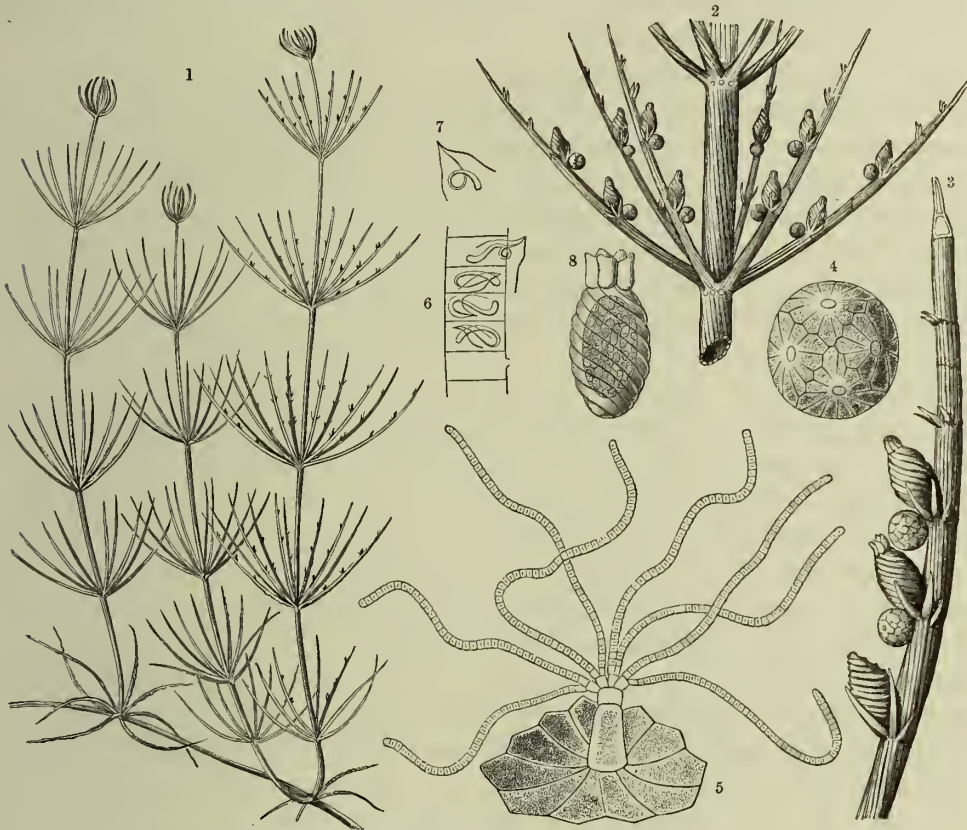


Fig. 206.—Fruit-formation in Stoneworts (Characeae).

<sup>1</sup> *Chara fragilis*. <sup>2</sup> Piece of the same with amphigonia and antheridia on the branches. <sup>3</sup> A single branch with amphigonia and antheridia. <sup>4</sup> An antheridium. <sup>5</sup> A plate of the antheridium with manubrium and cells grouped in the form of thongs and containing spermatozooids. <sup>6</sup> Several cells from one of the whip-like filaments; the cells in the middle contain each a spermatozoid, the spermatozoid is escaping from the uppermost cell, the lowest cell is already vacated. <sup>7</sup> A single spermatozoid. <sup>8</sup> Amphigonium inclosing the oogonium. <sup>1</sup> natural size; <sup>2</sup>  $\times 10$ ; <sup>3</sup>  $\times 15$ ; <sup>4</sup>  $\times 35$ ; <sup>5</sup>  $\times 100$ ; <sup>6</sup>  $\times 300$ ; <sup>7</sup>  $\times 500$ ; <sup>8</sup>  $\times 50$

closed, these manubria project towards the centre of the hollow sphere, and the rows of cells proceeding from the manubria are conglomerated into a ball. But as soon as the plates separate and the sphere falls to pieces, the ball is untwisted and its parts assume the appearance shown in fig. 206<sup>5</sup>. By this time a spiral spermatozoid has developed from the protoplasm in each of the discoid segments of the filaments, and may be seen lying within its cell (see fig. 206<sup>6</sup>). But almost immediately afterwards these cells open, and the spermatozooids, which are provided at one end with a pair of long cilia, escape and whirl about in the surrounding

water (see fig. 206<sup>7</sup>). The spermatozoids then pass through the fissures already described as existing beneath the crown of an amphigonium, and so reach the interior of the latter. Here, in the middle of the cavity is the oogonium (*i.e.* the great cell containing the ooplasm), and over it there is a slimy gelatinous mass, which occupies more particularly the neck of the amphigonium. The cell-membrane of the oogonium is attenuated and almost liquefied, and these soft and swollen masses of mucilage do not interfere in any way with the progressive motion of the spermatozoids. The latter reach the ooplasm, and, so far as we can see, a coalescence of the two kinds of protoplasm takes place.

The changes set up in the fruit-rudiment by fertilization first manifest themselves externally in an alteration in colour. The chlorophyll-bodies, hitherto green, assume a reddish-yellow tint; the spiral cells of the amphigonium become thickened and nearly black, and the amphigonium constitutes a hard shell which acts as an outer envelope inclosing the inner envelope of the fertilized ooplasm, now converted into an embryo. The entire structure next detaches itself from the stalk-cell, sinks under water, and remains for a considerable time—usually through the whole winter—lying unchanged at the bottom of the pond. The embryo does not germinate till the following spring, when it begins by developing a linear series of cells, the so-called pro-embryo, and from one of the cells of this pro-embryo is produced a Stonewort plant with branches in whorls as before (see fig. 206<sup>1</sup>).

The fruit-rudiment in Muscineæ (Mosses and Liverworts) exhibits in many respects a resemblance to that of a Stonewort, although its origin is quite different. It takes its rise from a superficial cell of the Moss-plant, and the cell belongs, according to the species, either to the foliaceous or to the cauline portion of the thallus. This cell projects in the form of a papilla above the adjoining cells, and becomes partitioned by a transverse wall into an under and an upper cell, the former of which serves as a pedestal to the body of tissue developed from the upper cell. The cellular body referred to is differentiated, by repeated insertion of longitudinal and transverse walls, into a central row of cells and an envelope. Amongst the central cells one situated somewhat low down in the series is conspicuous for its size; it contains the ooplasm, and must be looked upon as an oogonium. The central cells, which are placed in succession above it, are called the canal-cells of the neck. The name is derived from the fact that they occupy the constricted portion or neck of the envelope. The cellular envelope, which incloses the central row of cells and constitutes the amphigonium, is shaped like a flask (see fig. 191<sup>10</sup>); the lower, enlarged, ventral portion conceals the oogonium, the upper constricted portion is filled up by the neck-cells, and the whole structure, which received from the earlier botanists the name of "archegonium", is closed at the top by a lid composed of several cells. When the time for fertilization arrives the canal-cells of the neck swell up and are converted into mucilage. The lid-cells open and part of the mucilage is forced out; what remains offers no impediment to the admission of the spermatozoids to the ooplasm in the centre of the fruit-rudiment.



The antheridia arise in the same manner as the fruit-rudiments. A superficial cell of the thallus is enlarged into a papilla, and, by the repeated partition in all directions of its first segments, a body of tissue is produced, which includes a delicate stalk and a thickened upper portion, either clavate or spherical in shape. The latter part consists of a multicellular sac-like envelope and a parenchymatous filling-tissue inclosed within the envelope. In each cell of the internal tissue the protoplasm fashions itself into a spirally-bent spermatozoid, and shortly afterwards the entire filling-in tissue is resolved into its separate cells. The antheridium now opens at the top, and the loose cells with the mucilage in which they are embedded are ejected into the surrounding aqueous medium composed of rain or dew-drops. The spermatozoids then escape from their delicate cell-membranes, and swim about the water by the help of the two long cilia wherewith each is furnished (see vol. i. p. 29, figs. 7<sup>9</sup> and 7<sup>10</sup>). Passing down the open neck of the amphigonium, now filled with mucilage only, they succeed in reaching the oogonium in the enlarged base of the fruit-rudiment and apply themselves closely to its surface; a constituent portion of the spermatoplasm is absorbed into the ooplasm with the result that the latter becomes fertilized.

Usually several antheridia are situated close together. In Mosses they are mingled with paraphyses, structures resembling hairs, the significance of which has not yet been explained. In many species one individual develops only antheridia, another only amphigonia; but in other species antheridia and amphigonia are developed side by side on the same Moss-plant. Where the latter is the case either the oogonium exhibits an earlier development than the antheridium, or the reverse is the case. Either the passage leading to the oogonium through the neck of the amphigonium is opened whilst the adjacent antheridia are still closed, or else the spermatozoids are set free from the antheridia at a time when access to the oogonium is still barred by the lid-cells of the amphigonium. As in so many cases of a similar kind this contrivance prevents a union between the ooplasm and the spermatoplasm produced by the same individual, and favours cross-fertilization between different individuals.

In some Liverworts the antheridia and amphigonia are surrounded by annular walls, and these organs then appear to be sunk in depressions of the thallus. In other Liverworts separate lobes or branchlets of the thallus are transformed into stalked shields or discs, and the antheridia and amphigonia are formed in special niches and compartments on the surface of the shields. Those Muscineæ which have their thalli differentiated each into a cauline axis and cellular laminæ resembling leaflets, develop antheridia in the axils of the leaflets, or else in pitcher-shaped cavities at the tops of the stems. In Mosses the principal or secondary axes terminate in groups of antheridia or amphigonia, and specialized leaflets act as envelopes or roofs and constitute the "perichætium". Sometimes these leaflets have the appearance of floral leaves, as, for instance, in the Hair-Mosses (*Polypodium*), one species of which is represented in Plate IX. in the foreground to the left. The antheridia and amphigonia are here distributed on different individuals.

The investing leaflets at the summit of those stems which terminate in antheridia are crowded close together; they are short, broad, and of a brownish-red colour, and look like small floral-leaves seated upon a disc-shaped receptacle. *Polytrichum* is a typical instance of the Mosses which exhibit a conspicuous contrast between the investing scales of antheridia and those of amphigonia. The perichætium in individuals which produce only amphigonia possess an altogether different form and arrangement of parts from the corresponding structure in antheridia-bearing individuals. The difference is shown in Plate IX. The *Polytrichum*-stems, which are seen in the picture standing up behind those terminating in flower-like discs, have no antheridia, but send up slender bristles, on each of which is borne a spore-case. These, however, are the products of amphigonia, which lie concealed amongst the long green leaflets at the tops of the stems, and have there undergone fertilization.

As before said, there is a close resemblance between Muscineæ and Characeæ as regards the position of the ooplasm to be fertilized in the middle of the amphigonium, the genesis and form of the spermatozoids, and, lastly, the process of fertilization. But from the moment of fertilization the course of development is altogether different. The fruits of Characeæ become detached from the mother-plant, whereas those of Muscineæ remain in connection with it, and this connection is not merely mechanical but organic. The generation developed from the Moss-fruit continues to derive the nutritive substances requisite for its growth and completion from the mother-plant, and without the support of the latter it would inevitably perish. The word support may here be used in a wide sense; for the mother-plant is actually the bearer or stay of the new generation, which is produced from the ooplasm converted by fertilization into an embryo, and it may be compared to a tree with Mistletoe growing upon its boughs. In Characeæ the separate stages of development are always quite distinct; the stage of maturity in particular being characterized by the falling away of the fruit from the mother-plant. This is not the case in Muscineæ. Since no separation in space takes place, it is also difficult to establish time-limits and to say when the fruit has attained maturity, and the difficulty is increased by the fact that no sufficient indications are afforded by alterations of shape or colour. It is best to look upon the formation of fruit as being complete as soon as fertilization has taken place; from this moment the ooplasm must be considered to be an embryo, and its envelopes to be fruit-coats. Evidence in favour of this conception of the phenomenon is afforded by the circumstance that after the union of ooplasm and spermatoplasm development is arrested, and a period of repose ensues, whereas both before and afterwards the outward manifestations of change follow one another in rapid succession. A description of the subsequent changes has been already given (see pp. 15, 16), and we need only repeat here that the generation which springs from the Moss-fruit develops spores and, after having scattered them abroad, dies away.

The strongest likeness exists between the fruit-rudiments and antheridia of Muscineæ and those exhibited by Ferns, Horse-tails, Rhizocarps, and Club-Mosses,









MOSES AND LIVERWORTS.





all of which are classed together under the name of Vascular Cryptogams, on account of the presence of vascular bundles in their stem-structures and phylloclades. The first generation of these Vascular Cryptogams, whereon are developed the antheridia and fruit-rudiments, also resembles in an unmistakable manner the first generation in certain Liverworts.

In Ferns, which constitute the most extensive section of the Vascular Cryptogams, and may be taken as their type, the first generation makes its appearance in the form of a flat, green, foliaceous structure, usually reniform or heart-shaped, lying in close contact with the nutrient soil (see fig. 189<sup>16</sup>). Inasmuch as the tissue of this first generation nowhere contains vascular bundles, it must be looked upon as a thallus, and has received the name of *prothallium*. The Fern-prothallium bears the fruit-rudiments as well as the antheridia upon its under surface, which is in contact with the nutrient soil, and which adheres to it by means of a number of delicate hair-like suction-cells. Some Ferns develop the fruit-rudiments and antheridia on separate prothallia; others produce them both on the same prothallium. In the latter case the fruit-rudiments are situated near the sinus of the prothallium, and the antheridia on the part remote from the sinus. Each fruit-rudiment may be compared to a flask in shape, and arises from a superficial cell of the prothallium which is only slightly arched outwards. This cell is divided by the insertion of two partition-walls into three cells, each of which is again segmented in definite directions. From the uppermost cell is produced a tissue which forms the neck of the flask-shaped fruit-rudiment; the middle cell gives rise to three cells, of which the two upper, the canal-cells, occupy the neck, whilst the undermost one becomes the relatively large and subsequently rounded ooplast. The daughter-cells developed from the lowest primary cell take the form of an investing wall round the ooplast, or, to return to the analogy of a flask, constitute the wall of the ventrally enlarged portion of the flask. The protoplasm of the ooplast is the ooplasm, and is now to be seen surrounded by a pluricellular tissue, which, as in the case of Characeæ and Muscineæ, may be called an amphigonium. Only the neck of the amphigonium projects above the other adjacent tissues of the prothallium; the enlarged ventral portion is, as it were, sunk in the substance of the prothallium.

The antheridia are also developed from cells upon the surface of the prothallium. These cells project in the form of papillæ above the surrounding tissue and undergo division by the introduction of partition-walls. The outermost daughter-cell becomes enlarged and assumes a globular shape, and from the protoplasm in its interior are formed spiral spermatozoids. Another mode of origin consists in the formation of a papilliform or hemispherical protuberance of tissue which shows unmistakably a differentiation into central cells destitute of chlorophyll and enveloping cells containing chlorophyll. The former divide up and a filling-in tissue is formed, the small constituent cells of which contain spermato-plasm. After the development of a spermatozoid in each of these small cells, the whole of the filling-in tissue falls to pieces, that is to say, the individual cells separate from one another and remain for a short time disconnected but still in

contact. At length the top of the antheridium opens; the loose cells are discharged into the surrounding water derived from rain or dew, and from each of them is set free a spirally-coiled spermatozoid furnished as regards its anterior half with bristling cilia (see vol. i. p. 29, fig. 7<sup>11</sup>). The spermatozooids manifestly direct their course to an amphigonium as they whirl about in the water. Meanwhile the canal-cells of neck of the amphigonium have been partially converted into mucilage; some mucilage is discharged into the environing water, and it seems that concomitantly with this organic acids have been evolved in the region of the amphigonium, which exercise an attractive influence on the spermatozooids. What is known as a fact is that the spermatozooids accumulate in this mucilaginous mass and also penetrate through the slimy substance left behind in the canal of the amphigonial neck. Thus they reach the ooplasm which is hidden in the oogonium at the bottom of the fruit-rudiment. As it has repeatedly been observed that spermatozooids make their way into the ooplasm and there disappear, we may assume that the delicate envelope of the ooplast is pierced by the spermatozoid, and that thereupon a coalescence between the two kinds of protoplasm takes place (*cf.* also figs. 346<sup>1, 2, 3, 4</sup>).

The fertilized ooplasm now subdivides into several cells with partition-walls inserted between them, and thus is produced a multicellular embryo which remains embedded in the unaltered amphigonium. This structure, though scarcely differing at all from the fruit-rudiment, must be considered as a fruit. After a short period of rest the embryo germinates, and the new generation, which gradually makes its appearance as stem, roots, and fronds emerging from the embryo, continues for a short time to receive its food-stuffs through the mediation of the parental prothallium. At length, when the new generation has grown sufficiently strong, and is capable of taking up food-stuffs directly from the surrounding air and soil, and of transforming them into constructive materials, the assistance of the prothallium becomes superfluous. The prothallium then withers, and by the time the sporogenous fronds have developed it has vanished, and no trace of it remains.

The Horse-tails (*Equisetaceæ*) have, in the main, the same features as the Ferns just described as typical of the Vascular Cryptogams in all that relates to the forms of prothallium, antheridia, and fruit-rudiments. The prothallium produced from the spore is at first delicate and ribbon-shaped, but later becomes multifariously lobed, and in form recalls the thallus of certain Liverworts, or sometimes even resembles a little curled foliage-leaf. In most species antheridia and fruit-rudiments grow on different prothallia. Where this is not the case, fertilization of the ooplasm by spermatoplasm arising from the same individual is rendered impossible by means of a disparity between the organs concerned in respect of the time at which they mature. The prothallia which give rise to antheridia are always much smaller than those which produce the fruit-rudiments. The antheridia develop from superficial cells at the end or on the margin of the lobate prothallium, whilst the fruit-rudiments, on the other hand, are derived from superficial cells in the recesses between the lobes (see fig. 190<sup>8</sup>). The spermatozooids

have a spatulate enlargement at one extremity, and carry on the other, attenuated end a regular mane of extremely fine cilia.

Far more important are the characteristics which distinguish from Ferns the Rhizocarpeæ and Lycopodiales, especially the genera *Salvinia*, *Marsilia*, and *Selaginella*, in all of which the development has been studied with great care. The antheridia-bearing prothallia are, in the last-mentioned genera, extremely different in point of size from those which bear fruit-rudiments. Both prothallia, it is true, have spores for their starting-points, but these spores themselves have different dimensions, and are distinguished as *microspores* and *macrospores* (i.e. small spores and large spores). The microspores are the parts of the plant where antheridia are formed, and the macrospores those where fruit-rudiments are formed. In a microspore the protoplasm divides into several parts, and partition-walls are inserted between them, thus forming a tissue composed of a very few cells, the greater part of which remains concealed in the interior of the spore. Only one or two superficial cells of this tissue push out through rents made here and there in the coat of the spore, and these protruded cells constitute the antheridia. The apical cell of the antheridium becomes filled with a tissue, and in each cell of this tissue is formed a spirally-coiled spermatozoid. The opening of the antheridium and the escape of the spermatozooids then ensues in the same manner as in Ferns. The prothallium which originates from a macrospore and is the seat of formation of fruit-rudiments, although it is larger and composed of more cells than that just described, does not forsake the interior of the cavity of the macrospore to any greater extent, but only protrudes a little at one place where the tough outer coat of the macrospore is ruptured. Two kinds of tissue are in reality developed within the limits of each macrospore, viz.: the one above referred to as emerging between the torn edges of the outer spore-coat, and a tissue of reserve material deposited at the bottom of the macrospore. The latter is very rich in starch and oil, and serves as a storehouse of nutriment for the prothallium at least until it is in a position to get food for itself out of the environment. The fruit-rudiments (amphigonia) appear on the protruding portion of the prothallium, and are entirely buried in its tissue. The development of the fruit-rudiment, the formation of canal-cells which subsequently turn into mucilage, the penetration of the spermatozooids, and the act of fertilization, are in all essential respects the same as the corresponding processes in Ferns, and therefore a description of them in detail may here be dispensed with.

The tissue produced from a macrospore in the Rhizocarpeæ and Selaginellæ has been compared to the ovule as it occurs in the Phanerogams which will be the subject of the next chapter, and certain actual analogies have been brought out which are exhibited by the ooplasm when converted into an embryo, the store-chamber for food-stuffs, and the protective envelope in each case. Having regard to the identity of object aimed at through the instrumentality of these structures in the most widely different sections of the Vegetable Kingdom, such analogies are really a matter of course, and if naturalists limit themselves to proving that organs



which have the same functions, however greatly they may differ in form, yet always possess certain similarity, and that this similarity increases in a conspicuous degree when the external conditions of life are the same, no objection can be made to the generalization. But if it is made the basis of far-reaching speculations and of hypotheses concerning the evolution of one group of plants from another, the descent of Phanerogams from Cryptogams, for example, I must enter an emphatic protest against any such proceeding.

### THE COMMENCEMENT OF THE PHANEROGAMIC FRUIT.

Long experience has shown us that the propagation of plants is accomplished with much greater certainty by means of Brood-bodies than by Fertilization and production of Fruit. For a fruit to be formed, two portions of protoplasm which have arisen separately must be brought together. Such a union denotes that at least one of the two protoplasts in question is endowed with a capacity for translation, that the male cell is not obstructed on its way to the female, and that facilities are present to promote its union with that cell. But there's many a slip 'twixt the cup and the lip! Adverse winds, unfavourable currents, long-continued drought, uninterrupted rain, these and many another unexpected circumstance may bar the way to fertilization. Often enough fertilization is hindered from causes such as these, and in consequence the young fruit-rudiment atrophies, the embryo is not formed, and the plant, in order to propagate, must rely on its brood-bodies.

That fruits do not miscarry oftener than they actually do is due to the fact that the difficulties of the situation from external cause, are to some extent met by the position of the egg-cell and the form of the young fruit. In other words, the fashioning of the organs concerned in the production of fruit is adapted to the circumstances of the environment.

Perhaps the obstacles are at a minimum in the case of plants in which fertilization is accomplished under water. The cells in question here require no especial protection. The surrounding water maintains them in the proper position, brings food to them, and protects them from drying up. In it they both live and move. Thus it is intelligible why so many plants which live under water, or which use water for the accomplishing of fertilization, are destitute of any but the simplest envelopes for their spermatoplasm and ooplasm. Complicated investments are valueless under such circumstances, possibly even disadvantageous; in any case they are superfluous. Nor is it usual in plants to produce superfluous structures. As we know, aquatic plants do not possess woody stems and branches. And for this reason. Tissues of this kind are not required, since the surrounding water buoys them up in the proper position so that hard wood and bast are not needed. So also with the ooplasm and spermatoplasm. Cryptogamic plants which fruit under water do not possess complex ovaries like Phanerogams, as they are unnecessary. Just before the time of fertilization the

spermatoplasm is segmented up into many fragments; these escape from the antheridium and reach the simple fruit-rudiment by swimming. Since the spermatozoids are attracted to the young fruits by certain excretions which the latter pass out into the water, the multifarious devices associated with aërial fertilization are unnecessary. Protective coats around the sexual organs, sheaths to limit evaporation, brightly-coloured or sweet-smelling floral-leaves to attract insects that they may transfer the pollen from flower to flower—all these are wanting in plants which are fertilized under water. Now it is just these accessory protecting structures which constitute what are called blossoms. Thus we can say that these water-plants have no blossoms. To avoid misconception it must be stated that although they have no blossoms they have flowers. For although, popularly, blossoms and flowers are used as synonymous terms, under flowers are comprehended the organs which are concerned in fertilization, under blossom merely the leaves which inclose the essential organs and which guard and protect the young fruits and stamens. It is these latter which produce the sexual protoplasts. Their union is promoted by the leaves of the blossom. Sometimes they catch the pollen-grains as they are blown by the wind, or by the production of honey and scents attract insects which remove the pollen in their visits. In other cases, by projecting ridges and corners, they are instrumental in detaching the pollen from these same insects, and in a thousand ways protect and assist the difficult process of aërial fertilization.

In the above lines we have been speaking not of aquatic plants generally, but of such as are fertilized under water. And these should be carefully distinguished. Many aquatics, which pass their lives under water, send up their flowers to the surface so that their fertilization is aërial. On the other hand, strange though it may seem, the fertilization of most aërial Lichens, Mosses, and Ferns which grow on the sand of desolate moors, on the sunny rocks of mountain sides, or on the dry bark of old tree stems, is accomplished under water. Plants of this sort may be exposed to drought for many months, and the movement of sap within them may be suspended; but when they are moistened with rain or dew they are quickened and rejuvenated, and form their young fruits and antheridia. Things are so arranged that the liberation of the spermatozoids coincides with the moment at which these plants have access to sufficient moisture. Thus we see that it is literally true of these plants—whether growing on the bough of a tree or in a ravine on a mountain side—that their fertilization is accomplished under water.

The only really important distinction between plants permanently submerged and such as are thus situated from time to time, is that in the latter the young sexual organs are protected against desiccation during the periods of exposure by means of sheathing structures and leaf-like scales, as is particularly well shown by the Mosses. Blossoms in the usual sense, however, are not found amongst Ferns and Mosses, and we can make the following three general statements:—(1) That Cryptogams are fertilized under water and most Phanerogams in the air; (2) that

Cryptogams lack blossoms, since these are not necessary for aquatic fertilization; (3) that almost all Phanerogams, on the other hand, possess blossoms, since they are required to protect and promote aërial fertilization.

The very complicated structure of the parts immediately adjacent to the region where the sexual protoplasts are developed depends upon the fact that fertilization is aërial. The portions of protoplasm destined for fertilization can only be adequately elaborated if their enveloping membranes are thin and delicate, and suited for the osmotic transfer of materials. Such a membrane, however, is incapable of protecting the protoplasm from the drying influence of the air; it is absolutely essential that both the spermatoplasm and the ooplasm shall be protected during the critical period by a suitable envelope. Thus one finds in all Phanerogams—quite apart from the perianth—a protective mantle developed around the sexual cells. This mantle has its cell-walls suitably thickened; its outer layers afford the necessary resistance to desiccation, whilst deeper down an ample supply of water is maintained.

These characters are well shown in that constituent of the ovary from which the seed will be ultimately produced. This portion is known as the *ovule*. Every ovule consists of a mass of tissue, the *nucellus* of the ovule in which the ooplasm or egg-cell is concealed, and an enveloping sheath, the *integument*, which may be either single or double. Such ovules are borne in the genus *Cycas* (figs. 208<sup>7</sup> and 208<sup>8</sup>) without further covering than a fretwork of hairs which protects them against too great drying up. In other Cycads and in the majority of Gymnosperms, of which the Cypress and Juniper, the Pine and the Fir, may be quoted as examples, the leaf-like scales of the young fruit are so arranged that the ovules produced on their surfaces are hidden from view and secure against outside danger. In the other Phanerogams (the Angiosperms) the ovules are concealed in a closed chamber—the pistil—the lower enlarged portion of which is known as the *ovary*.

In the construction of this chamber the chief part is taken by the floral axis and by the floral-leaves known as *carpels*. So unequal, however, is the share taken by these parts in the structure of the ovary that in some cases it is formed almost entirely from the floral axis, and in others almost entirely from the carpels. In consequence the apex of the floral axis, which is known as the floral *receptacle*, shows an extraordinary variety of form. Thus in one series of plants the receptacle is not excavated, but solid, assuming the form of a knob, hemisphere, or cone (figs. 207<sup>8</sup> and 207<sup>9</sup>); whilst in others it is concave and excavated (figs. 208<sup>1</sup> and 208<sup>2</sup>). The forms met with in nature can be produced artificially by taking a conical mass of soft wax and flattening its summit, then gradually pressing it down into a saucer-like shape, and so on until one has produced a hollow bowl. So in nature we have at one extreme the solid cone, at the other the hollow vessel. Between these two extremes, between the conical and excavated receptacles, we have the flat or disc-like receptacle. It is hardly necessary to point out that in the growth and differ-



entiation of the living plant the excavated receptacle is not the result of any actual hollowing-out process as in the lump of wax, but is due to unequal growth of the different parts of the receptacle—the peripheral parts growing up as a circular wall around the central parts, so that the form of a cup or urn is gradually assumed. When one speaks of the excavation of the receptacle one is speaking figuratively—there is no excavation in a literal sense.

The configuration of the receptacle is further complicated by the fact that

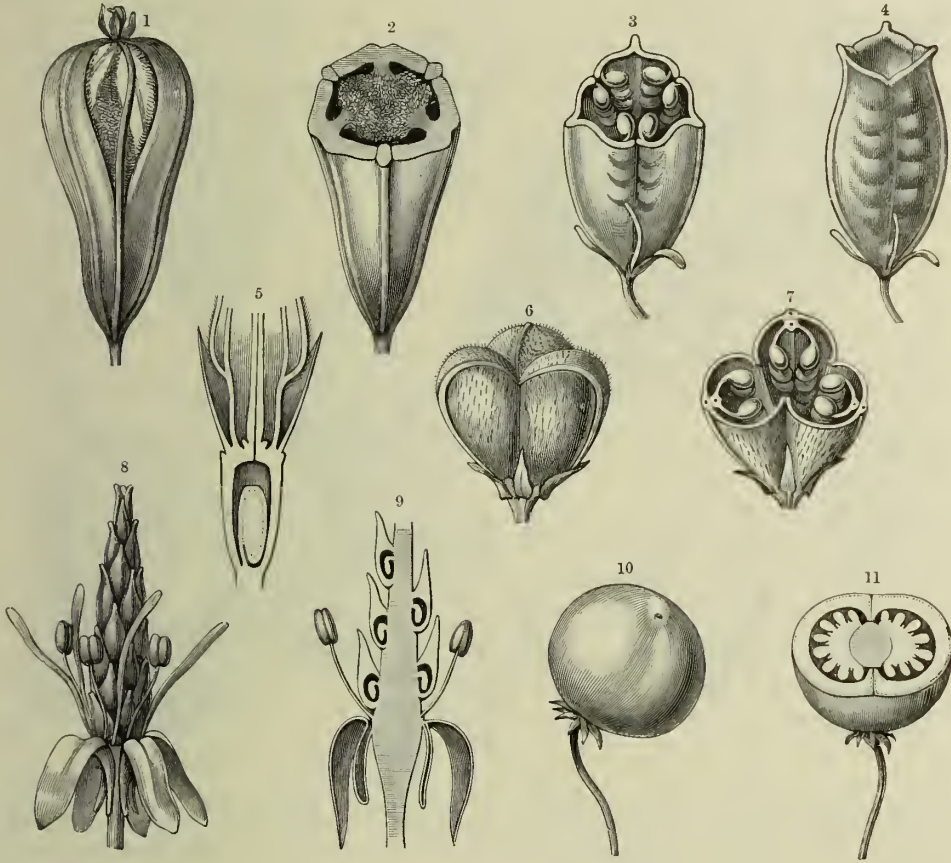


Fig. 207.—Structure of Phanerogamic Ovaries.

<sup>1</sup> Dehiscent fruit of *Miltonia stellata*. <sup>2</sup> Ovary of *Miltonia* cut across transversely. <sup>3</sup> Ovary of *Mignonette* (*Reseda*) cut across transversely. <sup>4</sup> The same ovary intact. <sup>5</sup> Longitudinal section of the ovary of the Jerusalem Artichoke (*Helianthus tuberosus*). <sup>6</sup> Ovary of the Violet (*Viola odorata*). <sup>7</sup> The same, cut across. <sup>8</sup> Receptacle and carpels of *Myosurus minimus*. <sup>9</sup> The same in longitudinal section. <sup>10</sup> Young fruit of Potato (*Solanum tuberosum*). <sup>11</sup> The same cut transversely. All the figures considerably magnified.

the centre of the receptacle does not always cease growing, but grows up as a cushion or peg; thus we have a receptacle having the form of a conical peg with a peripheral, urn-like wall around it.

In describing the relations of the floral-leaves to the receptacle it will be simplest to commence with the conical receptacle. Here the floral-leaves are found arranged in whorls above one another or in a continuous spiral. At the top are the carpels, below these the stamens, and below these again the leaves

of the perianth. Of these various kinds of leaves there may be developed one, two, or even more whorls. When several whorled carpels are united together so as to inclose a single chamber, the tip of the receptacle may be produced above the point of insertion of the carpels and project into the ovarian cavity, or it may penetrate the ovary as a central column. On the other hand, each carpel may give rise to a separate chamber, in which case one finds a whorl of distinct



Fig. 208.—Structure of Phanerogamic Ovaries.

<sup>1</sup> Excavated receptacle and carpels of a Rose (*Rosa Schottiana*). <sup>2</sup> The same in longitudinal section. <sup>3</sup> A single carpel of the same in longitudinal section. <sup>4</sup> Ovary of the Apple (*Pyrus Malus*) in longitudinal section. <sup>5</sup> The same in transverse section. <sup>6</sup> Transverse section of a ripe Apple. <sup>7</sup> Carpel of *Cycas revoluta* with ovules. <sup>8</sup> Longitudinal section of an ovule of *Cycas*. <sup>1</sup>, <sup>6</sup>, <sup>7</sup>, <sup>8</sup> natural size; <sup>2</sup>, <sup>4</sup>, <sup>5</sup>  $\times 3$ ; <sup>3</sup>  $\times 8$ .

ovaries at the tip of the receptacle (fig. 210<sup>7</sup>); or there may be numerous small ovaries spirally arranged around the receptacle (figs. 207<sup>8</sup> and 207<sup>9</sup>).

In order that the position and mutual relations of the various floral-leaves on disc-like and excavated receptacles may be intelligible it is necessary that we should return to the lump of wax. Let the cone of wax be pressed down so that it assumes the form of a disc or cup. Assuming the floral-leaves to be present upon it during this process—covering the cone from base to apex—when the disc stage is reached the leaves formerly present at the apex will occupy the centre, those at the base the periphery of the disc. If the wax be further moulded into a cup the leaves previously at or near the apex of the cone will

occupy positions within the cup—those immediately at the apex being at the centre—whilst those near the base will be found on the edge of the cup.

According as the leaves are inserted spirally or in whorls upon the receptacle, whether they are present in single or double cycles, whether they are fused with one another or with the receptacle—all these offer almost infinite possibility of variation in form, so manifold, indeed, that their complete description is quite beyond the limits of the present work. Here the forms described must be limited to a series of more or less typical cases; they are for the most part selected from well-known and widely-distributed plants readily accessible to any one.

To avoid repetition the seventeen selected cases are arranged in two groups, of which the first group includes forms with a conical receptacle, the second such as have a disc-like or excavated receptacle. Each of these groups is further subdivided, according as the carpels are all of one sort or of two sorts.

### OVARIES ON A CONICAL RECEPTACLE.

#### *Carpels all of One Sort.*

(1) The carpels are inserted spirally on the receptacle. Each carpel contains one or several ovules. The receptacle is either much elongated, as in the Mousetail (*Myosurus*, figs. 207<sup>8</sup> and 207<sup>9</sup>), or conical, as in the Tulip-tree (*Liriodendron*), or button-like, as in the Crowfoot (*Ranunculus*).

(2) The carpels are inserted in whorls upon the receptacle, their margins are infolded and fused with the prolonged apex of the receptacle. Since they are also fused with one another below, they collectively form a multilocular ovary. Each carpel bears ovules over its inner surface. As examples may be quoted the Yellow Water-Lily (*Nuphar*), and the Flowering Rush (*Butomus*, figs. 210<sup>7</sup> and 210<sup>8</sup>).

(3) The carpels are inserted in a whorl at the summit of the receptacle and are fused with one another. The receptacle does not project into the ovarian cavity. Each carpel bears ovules either along its margins, as in Mignonette (*Reseda*, figs. 207<sup>3</sup> and 207<sup>4</sup>), or on its internal surface, as in the Sundew (*Drosera*), or basally, as in *Dionæa*, *Drosophyllum*, and in *Caylusea* (Resedaceæ). In *Reseda* the ovary is open above.

#### *Carpels of Two Kinds.*

(4) The carpels arise at the tip of the receptacle in two alternating whorls of two each. The two upper carpels are reduced to midribs on which the ovules are borne in two rows. A delicate membrane is stretched like a tympanum between these two midribs which form the frame. The two lower carpels are destitute of ovules and are fixed like valves to the upper pair. This form is met with in numerous modifications in the Cruciferae.

(5) The carpels arise in two whorls at the tip of the receptacle. Those of the lower whorl are destitute of ovules and form the ovary, those of the upper whorl are modified into strings or cushions, and are fused with the inner surface of the



lower carpels. They bear the ovules. Examples:—the Violet (*Viola*, figs. 207<sup>6</sup> and 207<sup>7</sup>), the Celandine (*Chelidonium*), and the Poppy (*Papaver*).

(6) The lower whorl of carpels are united edge to edge, inclosing the ovarian cavity. They are destitute of ovules. The tip of the receptacle projects a very short distance into the ovary, and bears a single ovule-bearing carpel which is apparently terminal upon it. Examples:—the Rhubarb (*Rheum*), and Dock (*Rumex*, fig. 212<sup>23</sup>).

(7) The lower whorl of carpels are united edge to edge like staves, forming the ovary into which the apex of the receptacle projects as a central column. The upper ovuliferous carpels are metamorphosed into cushion-like structures consolidated with the receptacular column. These cushions are either arranged spirally, as in *Glaux* (figs. 211<sup>8</sup> and 211<sup>9</sup>), or in a whorl, as in *Primula Japonica*.

(8) The lower carpels are inserted in a whorl, and have their margins infolded, and are fused together so as to form a multilocular ovary. The upper, ovuliferous carpels arise from the tip of the receptacle, which is continued through the centre of the ovary. The ovules project into the cavities of the ovary. Examples:—The Spurge (*Euphorbia*), Azalea, Foxglove (*Digitalis*), Potato (*Solanum*, figs. 207<sup>10</sup> and 207<sup>11</sup>).

#### OVARIES ON A FLAT OR EXCAVATED RECEPTACLE.

##### *Carpels of One Sort.*

(9) The carpels are arranged spirally upon a raised central cushion of the *flat* receptacle. Each carpel forms a distinct ovary containing one or more ovules. Examples:—*Dryas*, *Potentilla*, the Raspberry (*Rubus Idæus*, figs. 210<sup>11</sup> and 210<sup>12</sup>).

(10) The carpels are arranged spirally within an *excavated* receptacle. Each carpel forms a distinct ovary containing one or more ovules. There is no fusion between the walls of the carpels and that of the receptacle. Example:—The Rose (*Rosa*, figs. 208<sup>1, 2, 3</sup>).

(11) A single ovuliferous carpel is inserted in the centre of an excavated receptacle. It is apparently terminal upon the axis, and is not fused with the excavated receptacle. This condition prevails in the Cherry, Plum, Apricot, and Almond (*Amygdalus*, figs. 209<sup>6</sup> and 209<sup>7</sup>).

(12) The carpels arise in a whorl from the end of the axis at the base of an excavated receptacle. Their margins are infolded, and they are fused together into a multilocular ovary. The ovary fills the whole cavity of the receptacle, with the inner wall of which it is fused. Ovules are borne by the infolded margins of each carpel. Examples:—The Medlar (*Mespilus*), Pears and Apples (*Pyrus*, figs. 208<sup>4, 5, 6</sup>).

(13) The carpels arise from the tip of the axis at the base of the excavated receptacle. The receptacle has a remarkable structure; it is like a bottle in shape with three portions of the wall removed, so that it is reduced to three ribs which join above and bear the other parts of the flower. The apertures in the receptacle are occupied by the three carpels. Thus the ovary consists of three carpels and

three receptacular ridges. The ovules are borne on longitudinally-running cushions on the carpels. This class of ovary is found in great variety amongst the Orchidaceæ (figs. 207<sup>1</sup> and 207<sup>2</sup>, and figs. 212<sup>1,2,3,4</sup>).

*Carpels of Two Kinds.*

(14) One series of carpels, destitute of ovules, arise from the margin of the deeply-excavated receptacle, roofing it in. Another series, metamorphosed into

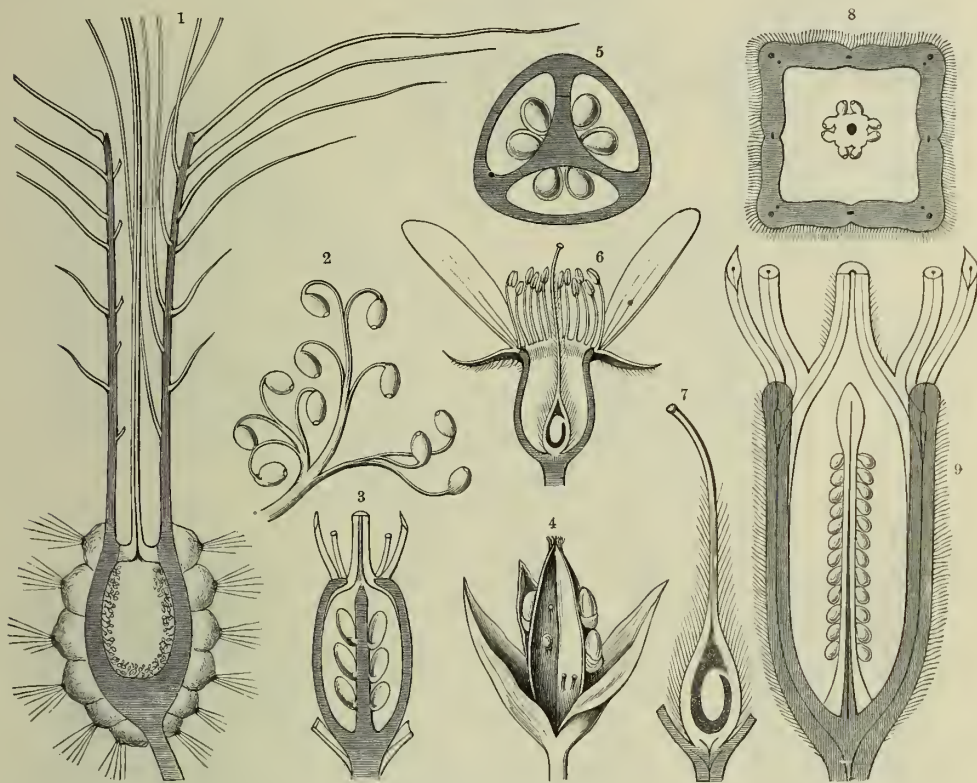


Fig. 209.—Structure of Phanerogamic Ovaries.

<sup>1</sup> Longitudinal section of the ovary of *Cereus grandiflorus*. <sup>2</sup> Ovules on a branched placenta from the base of the ovary of *Cereus*. <sup>3</sup> Longitudinal section of the ovary of *Hedychium angustifolium*. <sup>4</sup> Dehiscent fruit of the same plant. <sup>5</sup> Transverse section of the ovary of the same. <sup>6</sup> Longitudinal section of an Almond flower (*Amygdalus communis*). <sup>7</sup> Longitudinal section of the ovary of the same. <sup>8,9</sup> Transverse and longitudinal sections of the ovary of the Willow-herb (*Epilobium angustifolium*). <sup>1</sup> natural size; <sup>3,4,5,6</sup> slightly magnified; <sup>2,7,8,9</sup>  $\times 10$ .

ovule-bearing strings, arise spirally from the inner wall of the receptacle and project into the ovarian cavity. Examples are afforded by the Cactaceæ, e.g. *Opuntia* and *Cereus* (figs. 209<sup>1</sup> and 209<sup>2</sup>).

(15) One series of carpels closes the mouth of the excavated receptacle, as in (14). The other series, bearing the ovules, are filamentous, and arise as a whorl from the base of the receptacle; they are consolidated with a thread-like prolongation of the tip of the axis which runs up as a central column. Example:—The Willow-herb (*Epilobium*, figs. 209<sup>8</sup> and 209<sup>9</sup>).

[These two figures are slightly inaccurate in that the partitions of the ovarian cavity are not indicated. In the cross-section, fig. 209<sup>8</sup>, they would run diagonally from the corners to the central column. In allied forms they are sometimes incomplete.—*Ed.*]

(16) One series of carpels as in (14) and (15). The other series are metamorphosed into ovuliferous cushions spirally inserted on a continuation of the axis



Fig. 210.—Structure of Phanerogamic Ovaries.

1, 2 Antholysis or Chloranth of a Larkspur (*Delphinium cashmirianum*). 3 Ripe dehiscing fruit of same. 4 Longitudinal section of a single carpel of same. 5 Longitudinal section of an ovule of the same. 6 A single foliaceous carpel of same. 7 Pistil of *Butomus umbellatus*. 8 Pistil of same dissected. 9 Young ovule of same. 10 Full-grown ovule of same in longitudinal section. 11 Vertical section of flower of Raspberry (*Rubus Idæus*). 12 Longitudinal section of a single carpel of the same. 1, 2, 3 natural size; 4, 6, 7, 11 magnified 2-5 times; 5, 8, 9, 10, 12 magnified 6-8 times.

which rises up from the base of the receptacle. Example:—*Hedychium* (figs. 209<sup>3, 4, 5</sup>).

(17) As before, one series closes the mouth of the receptacle. From the tip of the axis at the base of the receptacle a single apparently terminal carpel arises which bears a single ovule. This condition obtains with many variations in the Compositæ, *e.g.* the Sunflower (*Helianthus*, fig. 207<sup>5</sup>).

The account of the structure of the ovary just given differs in several fundamental points from the current views of the best authorities in plant morphology. Especially is this so in two points. Firstly, in that the wall of



so-called "inferior ovaries" consists, for the most part, according to my own investigations, of a deeply excavated receptacle and not of carpels invested by the tube of the calyx or perianth. That the latter condition occurs (as in many



Fig. 211.—Antholysis and Structure of the Ovary.

1-6 Longitudinal sections of the ovaries of "monstrous" flowers of *Primula japonica*; the outer carpels form the ovarian cavity and are destitute of ovules; the inner carpels show all transitions between ovuliferous cushions, conrescent with the extremity of the axis, and isolated leaf-structures, the marginal teeth of which correspond to ovules. 7 A single "monstrous" flower of *Primula japonica*. 8 Longitudinal section through the ovary of *Glaux maritima*. 9 View into the ovary of same after removal of the front wall. 7 natural size; the others magnified 6-8 times.

Saxifrages) is not here denied, but more frequently is it the receptacle which is raised as a circular wall to form a closed ovary. On the ripening of the fruit the capsule in many cases opens by means of valves which strikingly resemble the valves formed from true carpels. It is, however, but a resemblance comparable to that existing between the phylloclades of Butcher's-broom and true leaves (*cf.* vol. i. p. 333).

A second divergence from recognized views is the assumption that two kinds of carpels take part in the formation of many ovaries, *i.e.* an outer series, destitute of ovules, forming the ovarian cavity, and an inner, ovuliferous series variously metamorphosed into cushions, strings, ridges, &c. This view is supported not only by extensive investigations into the development of ovaries, but also by a number of cases of antholysis which throw considerable light on obscure points of ovarian morphology.

As we shall refer frequently to this state of *Antholysis* it will be well to state at once, briefly, exactly what is meant by the term. Everyone is acquainted with the "double flowers" of Roses, Snowdrops, Carnations, Primroses, Tulips, &c., so common in cultivation. Into the cause of their origin we shall inquire later on; here it is sufficient to note that in double flowers we find (1) that the stamens are entirely or in part transformed into petals, occasionally into carpels; (2) that a multiplication of the perianth-leaves, stamens, and carpels is apparent, and (3) that with this change is often combined a *greening* of the parts not usually green, and (4) a general loosening and separation of parts which in ordinary, single flowers are fused with one another. Especially do we find those leaf-structures which normally are united to form the ovary loosened and increased; they are produced as flattened structures, having much the appearance of green leaves. One finds frequently all possible transitions in one and the same flower, so that the various stages in the conversion of carpels into green leaves can be readily followed.

In cases of antholysis where the parts of the ovary show a transformation into green leaves, one feels justified in regarding the structures in question as foliar in nature. Especially is this so when none of the ascertained facts of development militate against this view. In the same way such parts as never assume the forms of leaves in these "loosened" or segregated flowers may be interpreted as stem-structures—always provided that developmental history harmonizes with this view.

In the cursory review of types of ovarian structure given in the last few pages it was stated that in some cases carpels of one kind only are present, whilst in other cases carpels of two kinds contribute to the formation of the ovary. This statement is based in part on facts gleaned from an examination of these loosened, antholytic, or so-called "monstrous" flowers. The antholytic flowers of a Larkspur (*Delphinium cashmirianum*) reproduced in figs. 210<sup>1-6</sup> show unmistakably that only a single whorl of carpels is present and that each of them bears ovules on its margins. Similarly those of the Japanese Primrose (*Primula japonica*) represented in figs. 211<sup>1, 2, 3, 4, 5, 6, 7</sup>, demonstrate that here two sorts of carpels are concerned, *i.e.* outer foliaceous ones destitute of ovules, and inner ovuliferous ones modified into a cushion.

Having described the chief forms assumed by the ovarian cavity, we may pass on to speak of its most important contents, the *ovules*. All ovules agree in this: that at the time of fertilization they consist of masses of tissue, exhibiting a differentiation into central and peripheral cells, and also in the fact that one of the cells of the central portion is destined to become an embryo. In the majority of

flowering plants we find a definite central mass of cells, the *nucellus*, surrounded by a well-marked sheath, the coat or *integument*. Generally the integument is double, as in *Delphinium* and *Butomus* (cf. figs. 210<sup>5</sup>, <sup>9</sup>, <sup>10</sup>), in other cases it is single, as in *Compositæ*, *Umbelliferæ*, *Hippuris* and *Cycas revoluta* (cf. fig. 208<sup>8</sup>). In most Orchids the nucellus is inclosed in a large-celled, inflated and transparent integument, through which it is distinctly visible (cf. fig. 212<sup>5</sup>). In not a few epiphytic Orchids, however, this contrast of parts is only imperfectly shown, whilst in the *Balanophoreæ* and various other parasites no trace of the distinction into nucellus and integument is found. In all cases where an integument is present it is discontinuous at one point, where the nucellus is uncovered. This is the *micropyle*. Sometimes the micropyle is at the apex of the ovule, but in a very large number of cases the whole ovule is bent over so that the micropyle is situated close to the point of attachment of the ovule. The ovule may be attached to its support (*placenta*) by means of a filamentous cord, or it may be directly seated upon it. The common condition of an inverted ovule fused with its filamentous stalk is shown in figs. 208<sup>3</sup> and 210<sup>10</sup>. The filamentous stalk is technically known as the *funicle*, and the ridge where it is fused with the ovule as the *raphe* (cf. vol i. p. 644).

The cells of the nucellus of the ovule show a very unequal growth. One of them enlarges in a conspicuous manner, and is known as the *Embryo-sac*. In Conifers it attains relatively to the other cells of the nucellus enormous dimensions, whilst in most other flowering plants as it grows it encroaches upon the other cells of the nucellus till only a single layer remains surrounding it. And even this layer may be in part absorbed, so that the embryo-sac actually penetrates to the micropyle. The protoplasmic contents of the embryo-sac is richly vacuolated, but at the end directed towards the micropyle vacuoles are absent, and the protoplasm breaks up into several distinct protoplasts, each of which is provided with a conspicuous nucleus but in the first instance with no cell-membrane. As a rule three such protoplasts are found at the micropylar end of the embryo-sac; of these one only gives rise, after fertilization, to an embryo. This cell is the *ooplast* or "germinal vesicle", the other two are named *synergidæ* (cf. also, figs. 315 and 316).

In the ovaries of Orchids, as shown in figs. 212<sup>1, 2, 3, 4</sup>, the ovules arise in great numbers upon peculiar furrowed ridges of the carpels. They arise from the superficial cells of these ridges, and are not provided with any vascular-bundle connections; in fact, they are comparable to those epidermal structures known as hairs or trichomes. This analogy is emphasized by the fact that in the ovaries of many Orchids real hairs are present, as, for instance, in *Lalia Perrinii* and *Calogyne plantaginea*, transverse sections of which are represented in figs. 212<sup>1, 2, 3, 4</sup>. In these remarkable species six ridges project from the wall into the ovarian cavity, and from all of these hair-like structures are developed. The three ridges belonging to the curious excavated receptacle, already described, alone bear ordinary unicellular hairs, the others bear ovules, one of which is shown in fig. 212<sup>5</sup>.

The ovules of Cycads are very differently developed, as may be seen from a



reference to fig. 208<sup>7</sup>. Here no ovarian cavity is formed, the carpels are distinct from one another, and are spirally inserted upon the termination of the caudex; they are deeply lobed, certain of the segments being transformed into ovules.

Thus, while the ovules of Orchids seem to be equivalent to hairs, those of Cycads represent leaf-segments. In both cases the relations of the parts seem obvious. But in a great many cases the significance of the ovules is by no means so obvious, especially when the developmental history admits of various interpretations. In such doubtful cases antholysis offers a welcome assistance—that is, where this “loosening” and “greening” involves not only the ovary but also the ovules.

Especially valuable in this respect are certain cases of antholysis of the flowers of the Sundew (*Drosera*). Whilst in the normal flowers of this plant the ovules arise on the inner surface of the united carpels, in the foliaceous or antholytic ones they are borne upon the open and isolated carpels as glandular tentacles, like those usually occurring upon the leaves of this plant (*cf.* fig. 212<sup>6</sup>). On many of the carpels these glandular structures are fused together in little clusters (212<sup>7</sup>), and these fused structures show various transitional stages leading up to inverted ovules (figs. 212<sup>8, 9, 10, 11, 12</sup>). From a study of these cases one may infer that the integument of the ovule here is equivalent to a group of tentacles.

Very different is the case of the Larkspur (*Delphinium*). In normal flowers the ovules arise from the infolded margins of the carpels, each of which forms an ovary (*cf.* fig. 210<sup>4</sup>). But in the foliaceous flower the carpels are open and their margins lobed (*cf.* fig. 210<sup>6</sup> and fig. 212<sup>13</sup>). They recall the carpels of Cycas (fig. 208<sup>7</sup>) and agree with it in that some of the segments are converted into ovules. And it must be especially noted that the leaf-segments are so folded that a pit-like excavation is formed (*cf.* figs. 212<sup>14</sup> and 212<sup>15</sup>). Thus it appears that in the Larkspur the ovular integument is formed by the folding of the leaflet-like segments. Different again is the case of the Clover (*Trifolium*), of which an antholysis is shown in fig. 212<sup>16</sup>. The ellipsoidal ovules, which are borne along the fused margins of the infolded carpel in the normal flower, are here replaced by little, leafy structures resembling leaflets on the margin of the open carpel (*cf.* figs. 212<sup>16</sup> and 212<sup>17</sup>). These leafy structures are neither rolled up nor folded, and from each projects the nucellus of an ovule, or rather a mass of tissue corresponding to a nucellus, surrounded by an enveloping wall (*cf.* figs. 212<sup>18, 19, 20, 21</sup>). This wall may be regarded as representing the inner integument of the ovule, whilst the outer one is replaced by a leaflet. The monstrous ovules in the ovary of the Common Sallow (*Salix Caprea*, fig. 212<sup>20</sup>) show similar relations, except that the green, leafy structure upon which the nucellus of the ovule is inserted is folded along its midrib and has a fimbriated margin (fig. 212<sup>30</sup>). Of especial interest are the monstrous flowers of *Rumex scutatus* (*cf.* fig. 212<sup>24, 25, 26, 27, 28</sup>), a plant common on the débris slopes of limestone mountains. In the normal flower of this plant the ovary is egg-shaped, and consists of three carpels united edge to edge (figs. 212<sup>22</sup> and 212<sup>23</sup>). But in these monstrous cases it is enlarged from six to tenfold, and modified into a funnel-shaped tube open above (212<sup>24, 25, 26, 27</sup>). From this the ovule, also modified into a tube, sometimes



Fig. 212.—Ovules and Foliaceous Carpels.

<sup>1</sup> Transverse section of the ovary of *Lælia Perrinii*; natural size. <sup>2</sup> A portion of this section;  $\times 6$ . <sup>3</sup> Transverse section of the ovary of *Cælogyne plantaginea*. <sup>4</sup> A portion of this section;  $\times 6$ . <sup>5</sup> A seed of *Cælogyne plantaginea*. <sup>6</sup> Antholysis of the flower of Sundew (*Drosera intermedia*). (After Planchon.) <sup>7-12</sup> Isolated portions of this flower. <sup>13-15</sup> Isolated portions of a similar flower of *Delphinium elatum*. (After Cramer.) <sup>16</sup> Antholysis of *Trifolium repens*. <sup>17-21</sup> Isolated portions of the same. (After Caspary.) <sup>22</sup> Flower of *Rumex scutatus*. <sup>23</sup> The same flower in longitudinal section; magnified. <sup>24-28</sup> Isolated portions from an antholysis of *Rumex scutatus*. (Partly after Peyritsch.) <sup>29</sup> Longitudinal section through the pistil of a "monstrous" flower of *Salix caprea*. <sup>30</sup> Foliaceous ovule from this pistil. <sup>6-30</sup> slightly magnified.

projects (212<sup>24</sup>), or it may remain concealed within (212<sup>27</sup>). Inside the ovular tube arises a little protuberance which may be regarded as equivalent to the nucellus of

the ovule. It is sometimes attached to the wider end of the tube (212<sup>25</sup>), but more frequently it arises from the narrowed base as a tiny, conical projection inclosed in a circular envelope of its own (212<sup>23</sup>). This envelope corresponds to the inner, and the tube to the outer integument of the ovule.

From a study of these monstrous flowers it would appear that when the ovule possesses two integuments, the outer one corresponds sometimes to the whole apical portion of a carpel, sometimes to but a segment of a carpel; the former being the case when carpels of two kinds are present, and when, at the centre of the floral receptacle, above the outer non-ovule-bearing carpels, only a single fertile carpel is produced. The inner integument, on the other hand, arises like a corona from the leaf-like outer one.

The nucellus of the ovule arises in many instances (*e.g.* in Orchids) from a mass of tissue produced by the division of a single epidermal cell, but in by far the majority of cases at the margin or upon the surface of a leaf or leaf-segment, resembling in all respects a foliar bud.

That the ovule can be produced directly from the floral receptacle is not yet ascertained with certainty, though such an origin would appear to be not improbable in the Pepper family. That is no good reason why ovules should behave differently from bud-like brood-bodies, which arise sometimes from leaf- and sometimes from stem-structures. So great is the analogy between ovules and detachable buds, that ovules formerly received from Botanists the name of "seed-buds". In this connection it is very instructive to contrast the ovules in the ovary of certain Orchids with the foliar buds produced on the leaves of some of these plants. In *Malaxis paludosa* (*cf.* fig. 200<sup>5</sup>, p. 41) the foliar buds are found partly on the upper surface of the leaf, partly on the margins, forming in the latter case a fringe. They consist of a compact, central portion inclosed in a large-celled envelope which is so fashioned that the whole structure resembles an ovule (*cf.* fig. 200<sup>6</sup>). So striking is this resemblance, that anyone unacquainted with the fact that these buds arise from foliage-leaves would unhesitatingly regard them as ovules. Later on, of course, differences appear, in that in the ovule an independent embryo is produced, whilst the bud gives rise to a shoot, which must be regarded as a branch of the parent plant. This is, of course, an important distinction, and applicable to the majority of cases, though not quite to all. The parthenogenetically produced brood-bodies, to be treated fully by and by, have both the form of true embryos and occupy the same position in the ovule beneath the micropyle. Were it not known that the hard, indehiscent fruit (achene) of *Gnaphalium alpinum* (= *Antennaria alpina*), with the rudiment of another generation which it contains, is produced without the intervention of pollen, without fertilization, it would certainly not be apparent from its structure. From this we may conclude that the distinction between bud and ovule, between brood-body and fruit, cannot be based on purely structural characters, and that fruits and brood-bodies are sometimes interchangeable—facts of great importance in solving the question of the importance of fertilization in the origin of new species.



## STAMENS.

As the last patches of snow disappear from the fields, the Snowdrop raises its white bells, and the catkins of the Willow break through the bondage of their bud-scales; in the copses likewise, where the warm March sunbeams penetrate, the Hazel begins to blossom and sheds its powder. These are the signs that spring is coming, and that the long winter is over. For some time the flowers both of the Snowdrop and Hazel have been ready—in the Snowdrop under ground, wrapped up in sheathing leaves; in the Hazel on the twigs as short, cylindrical, dusky catkins. With the advent of spring the catkins stretch and their crowded flowers are separated, they becoming flexible and hang like golden tassels from the branches, swaying in the wind and giving off their clouds of dust.

To this powder, long known to be connected with the fruiting of plants, the name of flower-dust has been given. This term, suitable in so many cases, has been used in others for a substance which, although corresponding in function to the flower-dust of the Hazel, differs from it in appearance. The cells which take the form of dust in the Hazel assume in other plants the form of sticky, viscous lumps, of spindle-shaped masses or granulated bodies, to which the designation dust is quite inappropriate. Were the species of plants whose flowers do not produce dust but few the term could stand, but when we find belonging to this category many of the principal families of plants—ten thousand Composites, eight thousand Orchids, five thousand Labiates, four thousand Rubiaceæ, three thousand Papilionaceæ, and thousands of Umbellifers, Rosaceæ, Crucifers, &c.; that, roughly speaking, two-thirds of Flowering Plants do not produce dust, it is evident that the term cannot have a general application. Consequently, Botanists speak of *Pollen* and not flower-dust. It is true this word simply means flour, and that its selection has not been a very happy one. Still the term has entered into botanical terminology, where it will remain. It is given to all those cells produced in the flowers of Phanerogams, which contain the spermatoplasm.

Pollen, then, consists of cells which contain spermatoplasm, and may be compared to the antheridia of Cryptogams. A definite portion of the substance of certain leaves of the floral axis is appropriated to the production of Pollen. These leaves, known as *Stamens*, resemble the other leaves of the floral axis in that they are inserted in whorls, or one above the other in a much-flattened spiral. Very few species of plants possess only a single stamen in each flower. The majority of flowers contain stamens arranged spirally or in whorls. As a rule stamens are inserted according to the  $\frac{1}{3}$  or  $\frac{2}{5}$  system (*cf.* vol. i. pp. 399, 400). In many cases their number and insertion resembles that of the petals and carpels of the same flower, though more frequently there is a difference. Thus, in the flowers of the Tulip-tree (*Liriodendron*), whilst the perianth-leaves have a divergence of  $\frac{1}{3}$ , the stamens are arranged according to the  $\frac{1}{3}\frac{3}{4}$  system. In *Ranunculus* the leaves of the perianth are arranged on the  $\frac{2}{5}$  plan, the stamens on the  $\frac{2}{5}\frac{1}{1}$ ; in *Polygonum* the former on the  $\frac{2}{5}$ , the latter on the  $\frac{3}{8}$  system.

Since in every species of plant the number of stamens remains constant, thus in the Mare'stail (*Hippuris*) there is one, in Lilac two, in Iris three, in the Woodruff four, in the Violet five, and in the Tulip six stamens, their number has been made the basis of a classification of flowering plants at once convenient and popular, though not strictly scientific. In the well-known System of Linnæus plants are arranged into groups called Classes, in which the first class (*Monandria*) includes all forms with a single stamen, the second (*Diandria*) those with two stamens, and so on.

The aggregate of stamens in a flower is termed the *Andræcium*. As a rule the

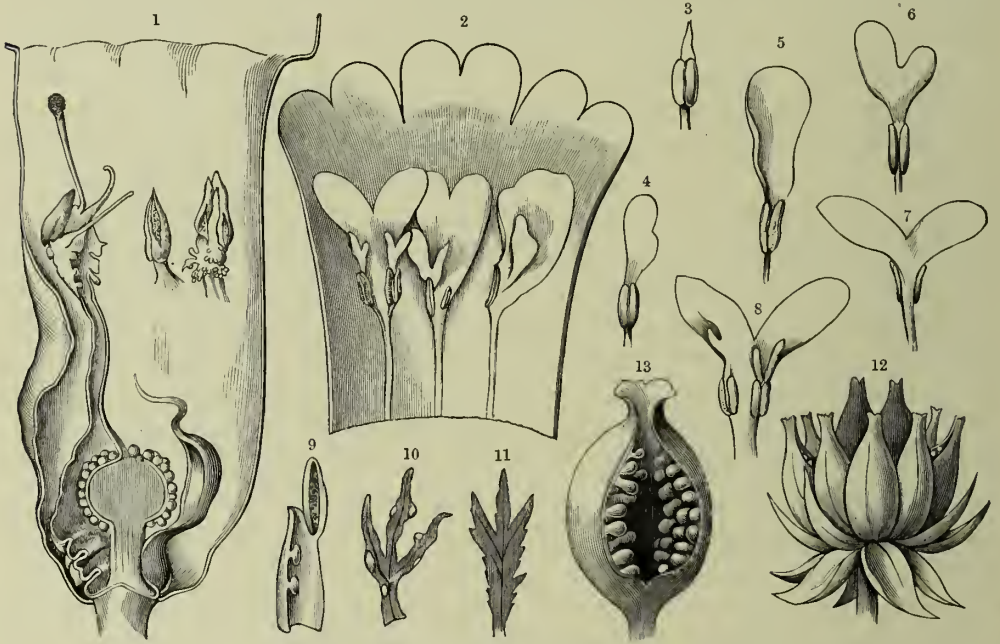


Fig. 213.—Stamens of double and monstrous flowers.

1 Vertical section of a green flower of *Primula japonica*. 2 Vertical section of a double flower of *Primula spectabilis*. 3-8 Isolated stamens from the same flower. 9 Stamen from a green flower of the Tiger Lily (*Lilium tigrinum*). 10, 11 Foliateous stamens from a flower of *Campanula Trachelium*. 12 Green flower of *Saxifraga stellaris*. 13 A single stamen from the same flower. (All the figures enlarged.)

andræcium is inserted between the leaves of the perianth and the carpels, so that from without inwards the sequence is perianth, stamens, carpels. Sometimes the carpels are wanting, so that the stamens constitute the inmost members of the flower; similarly also carpels may be present but no stamens.

We distinguish in a stamen that portion which is concerned in the production of Pollen—the *Anther*—and its stalk, the *Filament*. The stamens in many flowers are partly metamorphosed into petals; indeed, there are grounds for believing that all petals have been originally modified from stamens. What are known as “double flowers” are often flowers in which the stamens have given place to petals. All intermediate stages between stamens and petals can be seen in double-flowered Roses, Carnations, and Primulas (*cf.* figs. 213<sup>3, 4, 5, 6, 7</sup>). Not infrequently, at the

place where a petal narrows into its stalk or "claw", a little yellow swelling or callosity may be seen; this may be regarded as a reduced anther, and now and then it possesses the character of an anther, and contains actual pollen. It is frequently observed in double flowers that a multiplication of the leaf accompanies the con-



Fig. 214.—Stamens.

- <sup>1</sup> *Empleurum serrulatum*. <sup>2</sup> *Hypericum olympicum*. <sup>3</sup> *Juglans regia*. <sup>4</sup> *Soldanella alpina*. <sup>5</sup> *Viola odorata*. <sup>6, 7</sup> *Artemisia Absinthium*. <sup>8</sup> *Haminia* (after Baillon). <sup>9</sup> *Abies excelsa*. <sup>10</sup> *Euphorbia canariensis*. <sup>11, 12</sup> *Platanus orientalis*. <sup>13, 14</sup> *Juniperus Sabina*. <sup>15</sup> *Halicnocnemis gibbosa*. <sup>16</sup> *Halantium Kulpianum*. <sup>17</sup> *Sanguinaria canadensis*. <sup>18</sup> *Allium sphaerocephalum*. <sup>19</sup> *Actæa spicata*. <sup>20</sup> *Aconitum Napellus*. <sup>21</sup> *Salvia officinalis*. <sup>22</sup> *Viscum album*. <sup>23</sup> *Mirabilis Jalapa*. <sup>24</sup> *Tilia ulmifolia*. <sup>25</sup> *Thymus serpyllum*. <sup>26</sup> *Acalypha* (after Baillon). <sup>27</sup> *Bryonia dioica*. <sup>28</sup> *Ricinus communis*. <sup>29</sup> *Corydalis capnoides*. <sup>30</sup> *Polygala amara*. <sup>31</sup> *Doryphora* (after Baillon). <sup>32</sup> *Paris quadrifolia*. (All figures somewhat enlarged.)

version of stamens into petals. In the place of a single stamen we may find two stamens partially converted into petals, or there may be a greater number of petal-like leaves, standing one behind another, or, finally, we may have the appearance shown in figs. 213<sup>2</sup> and 213<sup>3</sup> of a double *Primula*.

By the action of parasitic Aphides and Insects stamens often assume a leaf-like appearance, they become green like the carpels described on p. 80. Such instances are of value in comparing the various parts of a stamen with those of the



hypothetic fundamental type of leaf-structure. At the first glance it might be supposed that the filament is a metamorphosed petiole, and the anther a metamorphosed lamina. But these monstrous flowers seem to indicate that such is comparatively rarely the case. Thus in the green stamens of *Campanula Trachelium* (figs. 213<sup>10</sup> and 213<sup>11</sup>) there are scattered everywhere over the green substance of the lamina yellow excrescences and warts containing reduced pollen-cells, and occasionally these occur fused together into actual portions of anthers; hence it may be inferred that in this case the anther may be regarded as equivalent to a green lamina. But far more frequently in such cases the pollen-producing tissue is found at the *base* of the lamina only, at the upper extremity of the leaf-stalk, where these two parts articulate. From this we may conclude that in the majority of cases anthers correspond to that portion of a leaf at which the stalk runs into the lamina. In such stamens the lamina is entirely suppressed, or is represented by a continuation above the pollen-producing region.

A few forms of this continuation above the anther, which we regard as representing a leaf lamina, are illustrated in fig. 214. Figs. 214<sup>1</sup> and 214<sup>2</sup> show it as a small shot-like grain, 214<sup>3</sup> as a truncate cone, 214<sup>4</sup> as a two-pronged fork, 214<sup>5, 6, 7</sup> as a flat, triangular scale, 214<sup>8</sup> as a toothed, sword-shaped process, 214<sup>9, 11, 12, 13, 14</sup> as a curved membraneous scale, 214<sup>15</sup> and 215<sup>16</sup> as a coloured bladder for attracting insects; and, finally, figs. 214<sup>31</sup> and 214<sup>32</sup> as a long, whip-like bristle.

That the filament of the stamen, or at any rate its lower portion, corresponds to a leaf-stalk seems so obvious, that it is hardly necessary to prove it by comparison with monstrous cases. Its name of *filament* indicates its character in a great number of flowers. Examples of these are Hemp, Hop, Wheat, Rye, Rice, Maize, Flax, and many others. For many cases no doubt the term filament is unsuited, as, for instance, in the thick, abbreviated stalks in the Violet and Bryony (figs. 214<sup>5</sup> and 214<sup>27</sup>). Similarly the filament may be strap-, spindle-, or club-shaped. The last is the case in *Thalictrum aquilegifolium*, *Bocconia*, *Sanguinaria*, and *Actaea spicata* (cf. figs. 214<sup>17</sup> and 214<sup>19</sup>), and it has been observed that the stamens very readily oscillate at the moment of liberation of pollen with the slightest breath of air. Like the foliage-leaves of the Orange, the stalks of which are provided with a peculiar joint, many Spurges and Labiates have hinged filaments (cf. figs. 214<sup>10</sup> and 214<sup>21</sup>). These hinges are wonderfully fashioned in many species of *Salvia*, reminding one of the articulation of the feet of insects; their importance in fertilization will be described in a later chapter. In the Linden the filament forks immediately below the anther (fig. 214<sup>24</sup>), whilst in *Corydalis* it is band-like, and divides into three (fig. 214<sup>29</sup>). In the Castor Oil Plant (*Ricinus*), and many other Euphorbiacæ, it is much divided and branched (fig. 214<sup>28</sup>). These *divided* filaments are not to be confused with *fused* ones, for occasionally we find that the filaments of adjacent stamens unite with one another into a ribbon or tube, as for instance in Mallows, Papilionacæ, and Polygalacæ (cf. 214<sup>30</sup>).

Attached to the sheath of foliage-leaves curious appendages, the stipules, are often found (cf. vol. i. p. 595). In the case of stamens these are but rarely met

with. They occur, however, in certain species of *Ornithogalum* (e.g. *Ornithogalum nutans* and *chloranthum*), in *Allium rotundum* and *sphærocephalum*, and in the Monkshood (*Aconitum*). Occasionally such staminal stipules are modified as honey-secreting glands at the base of the stamen, e.g. *Doryphora* (cf. figs. 214<sup>18</sup> and 214<sup>20</sup>).

It sometimes happens in monstrous flowers that the stamens are transformed into carpels, or we may find here and there an isolated stamen, which is partly so modified and partly still polliniferous. In such monstrosities it usually happens that it is the upper part which forms pollen, and the lower part which produces ovules (cf. figs. 213<sup>1</sup> and 213<sup>9</sup>). From this and other facts it has been inferred that the ovary corresponds really to the sheaths, the style to the petioles, and the stigma to the laminæ of the floral-leaves concerned. The monstrous flower of a Saxifrage (figs. 213<sup>12</sup> and 213<sup>13</sup>) shows that anthers and ovules can be produced from the same part of the leaf-stalk. This flower (213<sup>12</sup>) produces at the periphery five sepals and five narrow, green petals; in the centre two carpels (shaded dark in fig. 213<sup>12</sup>) as in normal Saxifrage flowers. Between the petals and carpels, i.e. where the stamens are usually found, there are ten structures which, whilst resembling both carpels and stamens to some extent, remind one forcibly of the excavated leaf-rachis of so many of the Pitcher Plants (cf. vol. i. pp. 125-133.) One of these is represented in fig. 213<sup>13</sup>. Its free extremity consists of an irregularly serrated scale, which may be compared either to a stigma or to the continuation of an anther, and may be regarded as the metamorphosed lamina. The excavated portion below may be regarded as the petiole. In its cavity are four rows of yellow protuberances, which might at first sight be taken for ovules. Closer investigation shows, however, that they contain pollen-mother-cells, each inclosing four pollen-grains. Here, then, we find the petiole consisting partly of carpel and partly of anthers, from which it may be concluded that that portion of the carpel which produces ovules corresponds entirely in position to the pollen-producing tissue.

The parts of the anther which produce Pollen in special chambers are known as *Pollen-sacs*, the tissue which binds these together as the *connective*. The connective is a direct continuation of the filament, and, like this, is penetrated by a vascular bundle. The pollen-sacs may be arranged like niches around the columnar connectives, which itself terminates in a sort of little shield, as in the Yew Tree (cf. fig. 234<sup>2</sup>), or they may be situated symmetrically right and left of it. In the latter case the pollen-sacs may lie at the edge of the connective in one place, as in the Juniper (figs. 214<sup>13</sup> and 214<sup>14</sup>), or they may be in pairs, i.e. two pollen-sacs to the right and two to the left of the connective (fig. 214<sup>3</sup>). This latter form is by far the most frequent, and occurs in certainly 90 per cent of all Phanerogams. It must be pointed out that the two pollen-sacs of each pair are separated from one another by a partition-wall only in the young anther. This disappears later on, and in the mature anther one finds, instead of four, only two sacs filled with pollen. Sometimes all four pollen-sacs run together in this way, by the breaking down of the parti-walls, as in Sundew (*Drosera*), Moschatel (*Adoxa*), *Monotropa*, and especially in *Globularia* (cf. figs. 216<sup>27</sup> and 216<sup>28</sup>). In

Orchids, on the other hand, the number of pollen-sacs is reduced to two, a number which remains unaltered at maturity.

The pollen-sacs in the anthers of the Mimoseæ are very curiously formed. In the anthers of *Acacia*, *Albizzia*, *Calliandra*, and *Inga*, there are eight spherical chambers in which pollen is produced, whilst in *Parkia* we find longitudinal rows of lenticular cavities in which balls of pollen lie embedded. The anthers also of the Rhizophoreæ show several longitudinal rows of such chambers, amounting in all to as many as thirty. The anthers of the Mistletoe (*Viscum*, fig. 214<sup>22</sup>) contain as many as forty to fifty pollen-chambers. In the majority of the Laurels (Lauraceæ) each anther is divided into four cavities, which stand in pairs, one above the other. As a rule, all four open towards that side by which insects visiting the flower for honey have to pass.

Many marked variations in the form of the anther are due to the relative dimensions of connective and pollen-sacs. Thus in the majority of Ranunculaceæ,

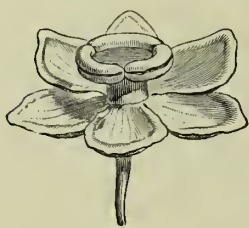


Fig. 215.—Curved anthers in the flower of *Phyllanthus Cycnanthera* (after Baillon).

Magnoliaceæ, Nymphæaceæ, and Papaveraceæ, the connective is broad, the pollen-sacs forming only a narrow rim to the anther (cf. fig. 214<sup>17</sup>). In the Skull-cap (*Scutellaria*), Calamint (*Calamintha*), Thyme (*Thymus*), and many other Labiates, as also in several Rosaceæ (*Rosa*, *Agrimonia*, &c.), the connective has the form of a three- to six-sided mass of tissue in which are embedded the spherical or egg-shaped pollen-sacs. Such anthers frequently resemble an insect's head with two lateral eyes.

It is not always possible to distinguish the limits of connective and filament, the whole stamen resembling a truncate column or anvil (figs. 216<sup>26</sup> and 216<sup>32</sup>).

Sometimes the connective assumes the form of a bar or lever running transversely to the filament, to which it is attached by a movable joint. This is notably the case in certain species of *Salvia*, to be described hereafter. Such a connective moves very readily upon its fulcrum. In many Liliaceæ (e.g. Tulips, Lilies, and Crown Imperials) and several Gentians (*Gentiana ciliata*, *nana*, &c.), the anther is united with the filament by an extremely delicate joint, so that the slightest touch sets it in vibration (versatile anthers). As examples of bulky pollen-sacs and much reduced connective, *Mirabilis Jalapa* (fig. 214<sup>23</sup>) and *Solanum Lycopersicum* (fig. 216<sup>2</sup>) may be quoted as examples.

It stands to reason that the character of the anther, indeed of the whole stamen, is correlated with the form of the pollen-sacs. All possible stages occur between globular and egg-shaped, and between egg-shaped and linear pollen-sacs. The drawings of sixty-four different stamens in figs. 214 and 216 give a good idea of the variety in this respect. Very curious are the curved anthers of *Phyllanthus Cycnanthera* (fig. 215), and those of *Acalypha*, which resemble a ram's horns (fig. 214<sup>26</sup>); the same remark applies to the undulating anthers of many Cucurbitaceæ, of which those of *Bryonia dioica* may serve as an example



(fig. 214<sup>27</sup>). There are forms allied to this last-named plant in which the anthers show very complicated convolutions—like those of the human brain.

When the time draws near for the pollen to leave its place of origin, its cells—whether in a loose powder or sticking one to another—become free from the inclosing wall of the anther, and lie embedded in the cavity of the pollen-sac, as it were in a purse or pocket, awaiting their release. The pollen-sac, hitherto



Fig. 216.—Stamens.

- <sup>1</sup> *Calandrinia compressa*. <sup>2</sup> *Solanum Lycopersicum*. <sup>3</sup> *Galanthus nivalis*. <sup>4</sup> *Cyclamen europæum*. <sup>5</sup> *Ramondia pyrenaica*.  
<sup>6</sup>, <sup>7</sup> *Cassia lenitiva*. <sup>8</sup> *Pyrola rotundifolia*. <sup>9</sup> *Arctostaphylos Uva-ursi*. <sup>10</sup> *Arctostaphylos alpina*. <sup>11</sup> *Vaccinium uliginosum*. <sup>12</sup> *Pyrola uniflora*. <sup>13</sup> *Medinilla* (after Baillon). <sup>14</sup> *Vaccinium oxycoccus*. <sup>15</sup> *Calceolaria Pavonii*.  
<sup>16</sup> *Tozzia alpina*. <sup>17</sup>, <sup>18</sup> *Sibbaldia procumbens*. <sup>19</sup> *Galeopsis angustifolia*. <sup>20</sup>, <sup>21</sup> *Erythraea Centaurium*. <sup>22</sup>, <sup>23</sup> *Melissa officinalis*. <sup>24</sup>, <sup>25</sup> *Calla palustris*. <sup>26</sup> *Nyctandra* (after Baillon). <sup>27</sup>, <sup>28</sup> *Globularia cordifolia*. <sup>29</sup>, <sup>30</sup> *Theobroma Cacao*.  
<sup>31</sup> *Pinguicula vulgaris*. <sup>32</sup> *Garcinia*. (All somewhat enlarged.)

closed, now opens, and the pollen is liberated. This opening or *dehiscence* of the pollen-sacs is accomplished in various ways. It has been already explained that most young anthers contain four sacs which rarely all remain distinct, but, by the breaking down of the parti-walls between each pair, become merged into two cavities.

These two cavities may be spoken of as anther-halves. In cases where the

four cavities remain distinct, a curious aperture is formed above each of them, as, for instance, in *Theobroma Cacao* (figs. 216<sup>29</sup> and 216<sup>30</sup>). When, however, the aforesaid fusion takes place (e.g. *Calla palustris*, figs. 216<sup>24</sup> and 216<sup>25</sup>), two openings only are formed. The anthers of *Globularia* have a very small punctiform connective and four pollen-sacs joined into an ellipsoidal body. After the disappearance of the parti-walls, leaving a single cavity occupied by pollen, a gaping, transverse slit arises, so that the anther is transformed into an open vessel (cf. figs. 216<sup>27</sup> and 216<sup>28</sup>). After the removal of the pollen the remains of the original parti-walls can be distinguished as two intersecting ridges. Similarly in the Butterwort (*Pinguicula*, fig. 216<sup>31</sup>) and in the majority of so-called one-celled anthers. In many Labiates, in which the anthers of adjacent stamens are in contact, and to some extent united together (syngenesious), the openings of the pollen-sacs in each anther unite, with the result that a pair of somewhat sinuous niches are presented, borne on the two curved filaments (cf. figs. 216<sup>22</sup> and 216<sup>23</sup>).

Dehiscence is accomplished sometimes by the formation of holes or pores, sometimes by slits. Of anthers with *porous dehiscence*, the greatest variety is exhibited by the Heath tribe and Pyrolaceæ. In the anthers of the Bilberry, Bog Vaccinium, Cowberry, and Cranberry (*Vaccinium Myrtillus*, *uliginosum*, *Vitis-idaea*, *Oxycoccus*), as also in Winter-green (*Pyrola*), the pouch-like pollen-sacs are drawn out into shorter or longer tubes, each of these tubes opening at its extremity by small circular pores (cf. figs. 216<sup>8</sup>, 11, 12, 14). But much more frequent is a dehiscence by means of *slits*. These are either longitudinal or transverse, or they may be sinuous or semicircular. When they are semicircular a valve or trap-door is cut out of the anther-wall.

At its first formation the slit resembles one cut by a sharp knife (cf. fig. 216<sup>1</sup>). In a number of cases the margins of the slit remain together, so that the aperture retains the form of a narrow crack; more frequently, however, the slit gapes, its margins roll up outwards or are folded back like a lid or folding-door. The *longitudinal slits* reach from end to end of the pollen-sacs (fig. 216<sup>1</sup>), or they may take the form of short gaping clefts near the free extremity of the anther. In the latter case (several examples of which are represented in figs. 216<sup>2</sup>, 3, 6, 7, 9, 10, 13, 15, 16), the slits very much resemble pores, from which they can only be distinguished in some cases by their mode of development. Occasionally the short, gaping clefts of adjacent anther-halves unite into a single opening, with a heart-shaped or rhomboidal outline, by which the whole of the pollen of both anther-halves escapes (examples are *Cyclamen* and *Ramondia*, figs. 216<sup>4</sup> and 216<sup>5</sup>). *Transverse slits* are met with most frequently in the stamens of Euphorbiaceæ, Cyclanthaceæ; also in a few Rosaceæ (*Alchemilla* and *Sibbaldia*, figs. 216<sup>17</sup> and 216<sup>18</sup>), in the Golden Saxifrage and Moschatel (*Chrysosplenium* and *Adoxa*), in *Globularia*, *Malva*, and others. On the whole, however, this method of dehiscence is rare. Of still rarer occurrence is that form of dehiscence in which semicircular slits arise in the anther-wall, producing valves or trap-

doors. This is known as *valvate dehiscence*. It is met with generally in Berberidaceæ (e.g. *Berberis* and *Epimedium*) and Lauraceæ. In the Bay Laurel, Camphor, and Cinnamon Trees (*Laurus nobilis*, *Camphora officinalis*, and *Cinnamomum*) and *Nyctandra* (fig. 216<sup>26</sup>) are found little apertures on one side of the stamen, each with its trap-door or valve, which is raised up in dry, but shut down in wet weather. The anthers of *Mimulus*, *Galeopsis*, and *Garcinia* (figs. 216<sup>19</sup> and 216<sup>32</sup>) resemble little tubs or boxes, which on opening raise their lid-like valves.

The dehiscence of the anthers in many plants is accompanied by yet other changes. The two anther-halves may become partly separated from their attachments and become twisted or diverge at right angles. If the anther-halves separate at the base only, as in *Convolvulus*, *Gentiana*, and *Menyanthes*, the anther assumes the form of an arrow-head; if they separate both above and below, and at the same time become somewhat bent, we have an X-shaped anther, found in many Grasses. In many Crucifers (*Diplotaxis*, *Sinapis*, &c.) the anthers become spirally twisted after dehiscence, a feature very pronounced in the Centaury (*Erythræa*, figs. 216<sup>20</sup> and 216<sup>21</sup>). A very striking phenomenon is the shortening which not a few anthers with longitudinal slits undergo after dehiscence. The anthers of most Liliaceous plants are long and linear; they dehisce by means of slits from above downwards. In the course of a few hours they are transformed into globular bodies, covered with pollen. In *Gagea lutea* these balls have a diameter only one-third of the previous length of the anther, whilst the anthers of the Crown Imperial (*Fritillaria imperialis*) shorten from 20 to 10, those of *Narcissus poeticus* from 11 to 4, and those of *Scilla bifolia* from 2 to 1 millimetres.

Each one of the various occurrences which accompany or succeed dehiscence depends upon some structural character of the anther-wall. The relations are simplest in those anthers which open by means of pores. The pores arise from the absorption of limited portions of the wall. Further changes, such as the shrivelling or shortening of the anther, or the expanding of the apertures, do not occur. There is a corresponding simplicity of the tissues of the anther-wall. Similarly, in anthers (e.g. Orchids) in which a splitting arises along a previously-indicated line, or in consequence of the absorption of a row of cells, no peculiarities are noticeable on the wall. But where slits with movable lips and valves are developed, cells of characteristic structure are present, which may be termed the contractile cells. One series consists of more or less cubical cells, and exhibit, on portions of their walls, fibrous or rod-shaped thickenings. The wall of one of these cells directed towards the cavity of the anther is equally thickened, that towards the outside is thin and delicate, easily folded, and destitute of thickenings. The side-walls, however, are characteristically strengthened by rod-like thickenings. The thickenings present may be compared to a hand, in the position usually employed in grasping an apple; the palm corresponds to the strongly-thickened inner wall, and the fingers to the tapering, rod-like thickenings of the



side-walls. As the cells dry a contraction of the rod-like thickenings supervenes, leading to a movement like that of the afore-mentioned hand when the tips of the fingers approach one another. Simultaneously the thin outer walls are thrown into folds, so that where a number of these cells are present, side by side, the whole outer surface will contract. These cells, being appropriately distributed over the wall of the anther, will cause the slit-margins to fold back or the valves to be raised. Besides these, other forms of contractile cells are present, differing from those described chiefly in form rather than in their mode of action.

It must suffice here to mention only a very few instances. The anther-wall in Conifers consists of a single layer of contractile cells, whilst that of *Agave* reaches the other extreme, there being six to eight layers of such cells present. As a rule the contractile layer is covered externally by a layer of delicate, thin-walled cells, known as the *Exothecium*; the contractile layer constitutes the *Endothecium*. The lining of the pollen-chambers consists of yet a third layer, the *tapetal cells*. In anthers which have dehisced this last-mentioned layer is rarely demonstrable, it having been already absorbed. Of the various layers it is the middle one, the endothecium (contractile cells), which is active in the various movements under discussion.

In the discharge of the pollen from the opened anthers a great variety of methods prevails. In the Nettle and Mulberry the filament of the stamen uncoils like a spring at the moment of dehiscence of the anther, and the pollen is forcibly scattered (fig. 229). The whole event is instantaneous, and to the observer resembles an explosion. In other plants dehiscence is accomplished quietly, and the pollen, which escapes slowly, may be first of all stored up temporarily at definite spots within the limits of the flower. This storage occurs a good deal more frequently than is generally supposed, and stands in relation to various events which will be fully discussed later on. In Papilionaceæ the liberated pollen is deposited in the hollowed apex of the *Keel*; in the Violet it is stored in the grooves of the lowest, spurred petal; in the Poppies, Roses, and Buttercups, it falls, at any rate in part, on to saucer-like depressions of the petals. The dust-like pollen as it falls from the anthers of the catkins of the Walnut, Hazel, Birch, and Alder, is received temporarily on the upwardly-directed under-surfaces of the flowers standing below (*cf.* fig. on p. 742, vol. i.). In Composites, Campanulas, and several Stellatæ, the pollen is stored on the style or stigma, but not, as was previously supposed, upon the receptive portions of this organ. On the contrary, it is retained here by various hairs and papillæ, specially designed for the purpose. Then, in the Proteaceæ again, the pollen is deposited, whilst the flower is still in bud, upon the summit of the stigma, without, however, coming into contact with the receptive spot; the stigma in this case serves, at the commencement of flowering, as a temporary dépôt for the pollen. In *Sarracenia* the pollen falls upon the stigma, which has the form of an expanded umbrella, and here for a while it remains, but not in contact with the receptive points. We shall hardly overstep the mark in saying that in some 20,000 species of plants

the pollen is temporarily stored in some portion of the flower and preserved for future use.

More frequently, however, the pollen remains within the opened anther. Usually these flowers are visited by insects which disturb the anthers and release the pollen, or they dust themselves over with it and carry it off to another flower.

The fact that the anthers are directed sometimes inwards, sometimes outwards, is correlated with these insect-visits. Where the slits or pores of the anthers are directed towards the periphery of the flower, one speaks of outwardly-directed anthers (extrorse), where toward the centre of the flower, of inwardly-directed (introrse). These relations are of importance in respect of insect-visits. If the honey is situated outside the whorl of stamens, the insects must pass between the stamens and petals to secure the nectar, as in *Colchicum*, *Iris*, *Convolvulus*, *Epimedium*, and *Laurus*. Here it will be advantageous for the anthers to be extrorse. On the contrary, when the honey is between the ovary and the bases of the stamens, and the insects have to penetrate to this region, as in *Gentians* and *Opuntias*, the stamens will be introrse. It is of great importance that the pollen exposed in the anthers should be rubbed off by the insects and carried to other flowers, a result only obtainable when the dehiscent side of the anther is placed in the way of the insect as it enters or leaves the flower.

Numerous other peculiarities affecting the structure, position, and movements of stamens will be dealt with later on, when treating of the removal of pollen from and to flowers by insects and other animals.

## POLLEN.

Like all other leaf-structures, stamens arise in the first instance as convex projections from their points of insertion on the stem. These projections consist of a homogeneous, small-celled tissue. They soon, however, assume a club-shaped form, and the outlines of anther and filament become recognizable. A vascular bundle is found traversing the entire length of each stamen, and the anther, which increases in size more rapidly than the filament, shows symmetrically-arranged, longitudinal grooves, with projecting portions between, arranged in pairs. The cells situated immediately below the surface of the young anthers become now marked out into tissues of two kinds. Towards the outside three layers of cells become distinguishable, and these, with the outermost, enveloping layer give rise to the wall of the anther; within, large cells become conspicuous, and form what is known as the *archesporium*.

These archesporial cells are arranged either in nests or in longitudinal rows embedded in the surrounding tissue. In the latter, the more usual, case, there are four, rarely two or eight, such rows arranged in pairs right and left of the central vascular bundle. Although at this stage of development all the cells of the anther hang together into a continuous mass, the existence of the future pollen-sacs—now

filled with the archesporial cells—is easily recognized. As time goes on the contrast between the wall of the anther and the contents of the chambers becomes more pronounced. The archesporial cells divide, giving rise to the pollen-mother-cells which entirely fill the pollen-sacs. Of the layers of the anther-wall, the inmost is usually dissolved, so that the mother-cells are bathed in a fluid mucilage; thus the wall comes to consist solely of the outmost, enveloping layer and of the contractile cells (“fibrous layer”) within.

Changes continue in the chambers or pollen-sacs, and in the partition-walls between them. The walls of the pollen-mother-cells become thickened, and often show a stratification. The protoplasm within divides into four parts, arranged frequently, though not invariably, in the corners of a 4-sided pyramid (*i.e.* in tetrads). Each of these cells becomes invested with a wall of its own, at first thin and delicate, but afterwards thickened and stratified. These are the pollen-grains. Their protoplasm possesses the property of a fertilizing agent, and is termed the *Spermatoplasm*.

In most plants a further division of the protoplasm in the pollen-cells takes place. This is conspicuous in the Conifers and Cycads, but relatively obscure in the majority of flowering plants. Of the two or more cells thus arising within the pollen-grain one only takes an actual part in fertilization.

How long the spermatoplasm retains its fertilizing properties unimpaired has not been sufficiently investigated. It has been stated of the plants enumerated below that this property is lost as follows:—

In <i>Hibiscus Trionum</i> ... .. after 3 days.	In the Larger Periwinkle ( <i>Vinca</i>
„ The Wallflower ( <i>Cheiranthus Cheiri</i> ) „ 14 „	<i>major</i> ) ... .. after 43 days.
„ „ Pansy ( <i>Viola tricolor</i> ) ... „ 26 „	„ <i>Pæonia pubens</i> ... .. „ 58 „
„ „ Bugle ( <i>Ajuga reptans</i> ) ... „ 32 „	„ <i>Pæonia tenuifolia</i> ... .. „ 65 „
	„ <i>Clivia nobilis</i> ... .. „ 76 „

It is by no means an unusual thing for gardeners to send the pollen of Cycads and Palms for fertilization to distant countries without its properties being impaired, provided it is kept dry during transit. The Arabs, who artificially pollinate the female flowers of the Date-palm, put aside some of the pollen from year to year, so that, in the possible event of the male flowers not developing, they may ensure a crop of dates. According to tradition, the pollen of Date-palms, Hemp, and Maize, can be used effectively for artificial pollination even after a lapse of eighteen years. Unfortunately, reliable investigations are wanting to show whether these accounts belong to the realm of gardeners' stories or not.

A great diversity obtains as to the manner of coherence of the pollen. When the walls of the mother-cells, containing the pollen-grains, become entirely absorbed, the pollen-sacs are filled with isolated cells, a condition which may be described as *free pollen*. Even now numbers of adjacent pollen-grains may cohere in clusters, in consequence of their possessing sticky coats or other arrangements. But in this case there is no suggestion of its being a real tissue, a difference of some moment.

In many plants, on the other hand, the pollen-cells remain, as they arose in the



mother-cells, united together in fours, and in this condition they leave the anther-cavities. These little pollen-aggregates are termed *tetrads*. Examples of such plants are:—the Ericaceæ (*Erica*, *Calluna*, *Menziesia*, *Andromeda*), the Bearberry (*Arctostaphylos*), the Strawberry Tree (*Arbutus*), the Alpine Rose (*Rhododendron*), *Ledum*, *Kalmia*, the Cranberry and Bilberry (*Vaccinium*); the Epacridaceæ, *Epacris* and *Leucopogon*; many Winter-greens (Pyrolaceæ); a few Sedges (*Juncus Jacquinii* and *Luzula vernalis*); finally *Anona*, *Drimys*, *Jussieuia*. In the plants just enumerated the tetrads correspond to the four pollen-cells in the corners of the mother-cell (*cf.* fig. 219<sup>2</sup>); but in the Apocynaceæ (*Apocynum*, *Periploca*), in numerous Orchids (*Ophrys*, *Spiranthes*), in *Fourcroya* (nearly related to *Agave*), and in several Bulrushes (*Typha Shuttleworthii* and *latifolia*), the four pollen-cells are arranged in one plane. In a few Willow-herbs (*e.g.* *Epilobium montanum* and *hirsutum*) the four cells are joined, but so slightly that they are readily separated on pressure.

Of much rarer occurrence than tetrads are *pollinia*. This name is given to the resultant mass of pollen-cells, when the whole of the pollen produced from a single archesporium (*i.e.* the whole contents of a pollen-sac) remain joined together into a tissue. A pollinium may consist of 8, 12, 64, or even many hundreds of pollen-cells. In the Mimoseæ the pollinia, which are found serially arranged, are lenticular, egg-shaped, or globular in form; in the Asclepiads they are spatulate, and consist of hundreds of pollen-cells. The pollen-masses of many Orchids are built up of numerous little clusters of pollen-cells, and show a branching or lobing; each of these clusters or lobes consists of greater or smaller pollinia. The masses, into which the pollinia of Orchids are aggregated, usually terminate in a stalk which is attached at its other end to a disc. This disc is so sticky that it readily adheres to any object coming in contact with it—a fact of significance in the conveyance of the pollinia from flower to flower by insects.

The dimensions of pollen-grains are very various in different groups of plants. Thus, whilst in the Forget-me-not (*Myosotis*), Borage (*Borago*), Comfrey (*Symphytum*), and Boraginæ generally, as also in Artocarpeæ (*e.g.* *Ficus*), the pollen-grains are very small, in Cannaceæ, Malvaceæ, Cucurbitaceæ, and Nyctagineæ, they are relatively large. The following table of diameters of pollen-grains shows the variation which exists in this respect:—

Millimetres.				Millimetres.			
<i>Myosotis alpestris</i> ,	...	...	0·0025–0·0034	<i>Viola tricolor</i> ,	...	...	0·062–0·071
<i>Lithospermum affine</i> ,	...	...	0·0042–0·0052	<i>Convolvulus sepium</i> ,	...	...	0·076–0·084
<i>Ficus pumila</i> ,	...	...	0·0045–0·0056	<i>Geranium Robertianum</i> ,	...	...	0·085–0·094
<i>Carinthe minor</i> ,	...	...	0·0050–0·0057	<i>Opuntia cynanchica</i> ,	...	...	0·15 –0·20
<i>Echium vulgare</i> ,	...	...	0·010 –0·014	<i>Oxybaphus nyctagineus</i> ,	...	...	0·18 –0·22
<i>Pilea microphylla</i> ,	...	...	0·018 –0·020	<i>Morina Persica</i> ,	...	...	0·19 –0·24
<i>Rhamnus cathartica</i> ,	...	...	0·022 –0·032	<i>Cucurbita Pepo</i> ,	...	...	0·20 –0·23
<i>Syringa vulgaris</i> ,	...	...	0·024 –0·034	<i>Mirabilis longiflora</i> ,	...	...	0·20 –0·24
<i>Aloe denticulata</i> ,	...	...	0·035 –0·050	<i>Cucumis Melo</i> ,	...	...	0·20 –0·24
<i>Yucca angustifolia</i> ,	...	...	0·055 –0·065	<i>Mirabilis Jalapa</i> ,	...	...	0·22 –0·25

The pollen-grains of the Marvel of Peru (*Mirabilis Jalapa*) are consequently

a hundred times greater than those of the Alpine Forget-me-not (*Myosotis alpestris*). It appears also that in many flowers which remain open but a single day or night, as, for instance, the Gourd and Melon, *Portulaca*, *Morina*, and the various species of *Mirabilis*, the pollen-grains are especially big. In a single anther-cavity of *Mirabilis Jalapa* there are, on the average, 32, and in one of *Borago officinalis* 60,000 pollen-grains.

In form pollen-grains are generally ellipsoidal (cf. figs. 217<sup>13</sup> and 217<sup>14</sup>), at



Fig. 217.—Pollen-grains.

<sup>1</sup> *Cobæa scandens*. <sup>2</sup> *Morina Persica*. <sup>3</sup> *Cucurbita Pepo*. <sup>4</sup> *Passiflora Kermesina*. <sup>5</sup> *Circæa alpina*. <sup>6</sup> *Convolvulus sepium*.  
<sup>7</sup> *Cannabis sativa*. <sup>8</sup> *Pinus Pumilio*. <sup>9</sup> *Mimulus moschatus*. <sup>10</sup> *Albucca minor* (dry and moistened). <sup>11</sup> *Dianthus Carthusianorum*. <sup>12</sup> *Corydalis lutea*. <sup>13</sup> *Gentiana rhatia*. <sup>14</sup> *Salvia glutinosa*. 1-3  $\times 80-90$ ; 4, 5, 7, 8, 10  $\times 120-150$ ; 11, 12  $\times 180$ ; 6, 9, 13, 14  $\times 220-250$ .

any rate in quite half of all flowering plants. More rarely are they spherical (figs. 217<sup>1, 3, 4, 6, 7</sup>). In the liliaceous *Tritelia* they are narrow and lancet-shaped, and in *Morina* (fig. 217<sup>2</sup>) biscuit-shaped. In the Pine the pollen-grain possesses two hemispherical bladders, and resembles an insect's head with two huge eyes (fig. 217<sup>8</sup>). In *Crucianella latifolia* they are barrel-shaped, and in *Brugmansia arborea* shortly cylindrical. Next to the ellipsoidal form, the angular or crystalline is the commonest. Thus the pollen-grains of the Nasturtium (*Tropæolum*) are 3-sided prisms, those of the Pansy (*Viola tricolor*) 4 or 5-sided, and those of Lady's

fingers (*Anthyllis vulneraria*) short 6-sided prisms with striated angles. A cubical form obtains in the pollen-grains of *Triopteris brachypteris* and *Basella alba*, that of a pentagonal dodecahedron in *Banisteria*, *Rivina*, and, in particular, in a number of Caryophyllaceæ, e.g. *Arenaria*, *Silene* and *Dianthus* (cf. fig. 217<sup>11</sup>). In the Dandelion (*Taraxacum officinale*), and in *Corydalis lutea* many crystalline forms occur, side by side, in the same anther (cf. figs. 217<sup>12</sup> and 218<sup>4</sup>). The tetrahedron, also, is not infrequently met with. This form occurs in *Thesium*, *Cuphea*, many Proteaceæ and Composites, sometimes with flat, sometimes with curved surfaces (cf. fig. 218<sup>6</sup>). A form, made up as it were of two spherical triangles joined together, occurs in *Circeæ* and many other Onagraceæ (fig. 217<sup>5</sup>).

The above paragraph relates solely to the varieties in form of dry pollen-grains. In the great majority of cases the grains are variously striated and grooved. In ellipsoidal and spherical grains, the grooves run like meridian-lines, so that two

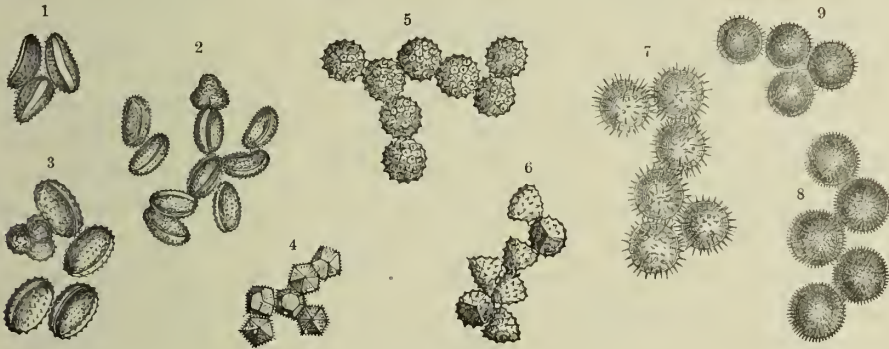


Fig. 218.—Pollen-grains.

<sup>1</sup> *Nymphæa alba*. <sup>2</sup> *Viscum album*. <sup>3</sup> *Carlina acaulis*. <sup>4</sup> *Taraxacum officinale*. <sup>5</sup> *Cirsium nemorale*. <sup>6</sup> *Euphthalmum grandiflorum*. <sup>7</sup> *Hibiscus ternatus*. <sup>8</sup> *Malva rotundifolia*. <sup>9</sup> *Campanula persicifolia*;  $\times 200$ .

poles are distinguishable. The number of the grooves is constant for a given species, and even for whole families of plants. A single furrow is characteristic of the grains of the Tulip-tree, Magnolias, and Water Lilies (fig. 218<sup>1</sup>), of the Meadow Saffron, Tulip, Lily, Iris, Narcissus, and Snowdrop, of Palms, Grasses, and, indeed, Monocotyledons generally. Two furrows are found on the pollen-grains of *Calycanthus*, several climbing Smilacineæ (*Tamus*, *Dioscorea*), and several species of *Amaryllis*. A very great number of plants have three grooves, e.g. Rock-roses, Violets, Poppies, Ranunculaceæ, Roses, Almonds, many Papilionaceæ, Beeches, Oaks, and Willows, Solanaceæ, Gentians, Scrophulariaceæ, and many Composites (cf. figs. 217<sup>13</sup> and 218<sup>3</sup>). Four grooves have been noticed in several Boragineæ (*Anchusa*, *Nonnea*), some Labiates (*Teucrium montanum*, *Sideritis scordioides*), in *Houstonia*, *Platonia*, *Blackwellia* and *Cedrela odorata*; six in most Labiates (fig. 217<sup>14</sup>), nine or ten in *Sherardia*, *Borago*, and *Symphytum*; twelve in *Crucianella latifolia*; sixteen in *Polygala chamæbuxus*; twenty-one to twenty-three in *Polygala myrtifolia*. On crystal-like pollen-grains the grooves are extremely delicate, and their number depends on the number of angular ridges.



A very conspicuous feature of many pollen-grains is the infinitely varied sculpturing, &c., of their walls. Sometimes this takes the form of a delicate dotting of the wall, as in *Asarum*, Meadow Saffron, Rue, Salvia, Gentians, and Euphorbias, many Aroids and Musaceæ (cf. figs. 217<sup>13</sup> and 217<sup>14</sup>); or the projecting ridges may be transversely striated as in *Saxifraga aizoides*; or, again, delicate striations may run in meridian-like circles (e.g. *Brugmansia arborea*). Sometimes dotted lines are found arranged in various ornamental reticulating patterns. On the smooth surface of the grains of *Thesium alpinum* and *rostratum* reticulations occur, and in the centre of each mesh a distinct dot. Similarly in Thrift and Sea Lavender (*Armeria* and *Statice*), and in the Corn Cockle (*Agrostemma Githago*). Often the surface presents considerable unevenness. In *Cuphea platycentra* the outer coat is prettily ridged, whilst in many other cases it is finely granulated. The little projecting granules may be either scattered equally over the whole surface, or they may be arranged in networks—which is specially the case in Cruciferæ (*Capsella*, *Raphanus*, *Sinapis*). In the Passion Flowers (e.g. *Passiflora Kermesina*, fig. 217<sup>4</sup>) these networks are inclosed in shallow, ring-like depressions, whilst in *Cobæa scandens* (fig. 217<sup>1</sup>) the surface has a honey-combed appearance. Sometimes the whole surface is dotted over with little wart-like projections, as in *Centaurea Jacea*, Mistletoe (*Viscum album*), White Water Lily (*Nymphaea alba*), and the tropical Bauhinias (*Bauhinia armata*, *furcata*, cf. figs. 218<sup>1</sup> and 218<sup>2</sup>); or it may be covered with sharp, needle-like prickles, as in the pollen-grains of Composites, Scabiousses, Campanulas, Cucurbitaceæ, Malvaceæ; also in the genera *Armeria*, *Amaryllis*, *Canna*, *Lonîcera*, *Ipomœa*, and *Convolvulus* (cf. figs. 218<sup>3</sup> and 218<sup>9</sup>).

It is only the superficial layer of the pollen-grain which shows these sculpturings and projections, the inner layer, which abuts immediately upon the protoplasm, is homogeneous. The wall of pollen-grains is, as a rule, three-layered. These three layers are:—the internal one or *intine*, the middle one or *extine*, and the external one or *perine*. The extine and intine arise from the protoplasm of the pollen-cell itself; the perine, on the other hand, is deposited from the matrix in which the young pollen-grains lie embedded. It comes about in this way. The young grains first clothe themselves with delicate walls, which are in due time thickened. This is the extine. Within this they form a second layer, the intine. Lastly, the perine is deposited upon them from without. The intine and extine can generally be readily distinguished as separate layers, but between the extine and perine the boundary is by no means so well marked. The various sculpturings, prickles, and other unevennesses of the outer coat really appertain to the perine.

It sometimes happens at definite spots on the wall of a pollen-grain, from a separation of the molecules there, that little spaces or actual canals arise which open externally by tiny pores. This may be well observed in *Thesium*, *Prunella*, *Ipomœa*, and *Gentiana*. In these canals a yellow (rarely colourless) oil is contained, which oozes out in the form of minute drops when the grains are moistened and absorb water. Such at any rate is the behaviour in *Prunella grandiflora* and *Gentiana ciliata*. In many other plants the whole surface of the grain is saturated

with this oil. I ascertained that in about 400 out of 520 species investigated by me the outer surface was overlaid with oil. The layer is so thin that with dry pollen-grains it is not visible, but when they are placed in water, the coating is resolved into a number of minute, strongly-refracting droplets, which adhere to the swollen pollen-grains like tiny beads. There is no doubt that this coat consists of a fatty oil, since it is soluble in alcohol and olive-oil, and with osmic acid it turns dark-coloured and becomes congealed.

More rarely are pollen-grains found with masses of a sticky, structureless substance adhering to them. This substance does not form droplets with water, nor does it dissolve in alcohol and olive-oil. It may be termed *Viscin*, from the similarity which it presents to the bird-lime obtained from the berries of the

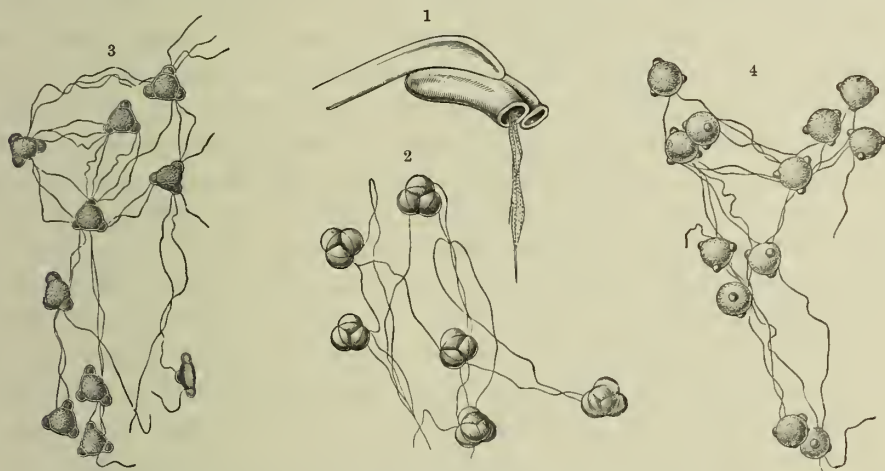


Fig. 219.—Pollen-grains and pollen-tetrads united by threads of viscin.

1, 2 *Rhododendron hirsutum*. 3 *Enothera biennis*. 4 *Epilobium angustifolium*. 1×8; 2-4×50.

Mistletoe (*Viscum*). Such a viscin is met with on the surface of the pollen-grains of *Fuchsia*, *Clarkia*, *Circeæ*, *Gaura*, *Godetia*, *Enothera*, *Epilobium*—indeed, throughout Onagraceæ and in Azaleas, Rhododendrons, Orchids, and Asclepiads. It is very sticky, and on the slightest touch can be drawn out into delicate threads. The contents of the anthers, as they escape, in the Evening Primrose (*Enothera*) and Willow-herb (*Epilobium angustifolium*) resemble fringes and tattered ribbons, or a broken net hanging from the adjacent anthers. Under the microscope this substance is seen to consist of pollen-grains, joined together by the sticky strings of viscin (fig. 219<sup>3</sup> and 219<sup>4</sup>). The phenomenon is even more striking in the numerous species of *Rhododendron*. In *Rhododendron hirsutum* all the pollen-tetrads of an anther-cavity are held together by a mass of sticky viscin. The anther dehisces by two terminal pores, and from these the pollen-tetrads ooze out to some extent. If the sticky mass be touched with a bristle it adheres, and the whole contents of the anther can be readily withdrawn (fig. 219<sup>1</sup>). Its appearance under the microscope is shown in fig. 219<sup>2</sup>. In many species, as for instance in the elegant *Rhododendron Chamæcistus* of the Northern Limestone Alps, and in the large-flowered Himalayan

species, strings and filaments are woven from the anthers a centimetre long, and insects visiting the flowers touch the strings, stick to them, and carry off with them to another flower generally the whole of the contents of the anther in question. The sticky substance is probably a mucilage formed from the outer wall of the pollen-tetrad, or from the broken-down walls of the mother-cells.

Not to be confused with the little pores communicating with the canals containing the oil are the thin portions of the outer layer, into which the intine projects, cæcum-like, as it swells up in water. It often looks as though the extine were actually perforated at these places; this, however, is not the case, and it is not till later, when the intine pushes through and the pollen-tube is formed, that these places are burst and true apertures arise.

The variety exhibited by these spots is as remarkable as that of the sculpturings. The outmost layer often thins out at those spots where the wall is grooved. As the grain swells up in water, the extine often bursts at the thin region, and may actually peel off (*cf.* fig. 217<sup>10</sup>). In *Mimulus* and *Thunbergia* the thin region has the form of a spiral, or it may run into loops and convolutions, as shown in 217<sup>9</sup>. When the intine swells up and bursts the extine, the pollen-grain looks as though it had been pared. In the Passion-Flower the thin places are ring-like, so that with the swelling of the intine, the extine comes away in the form of little lids. The same thing happens in the Gourd, where the lids are very small, and are provided each with a little spine (fig. 217<sup>3</sup>). A curious condition obtains in *Morina Persica* (allied to the Teasel, *cf.* fig. 217<sup>2</sup>). Each of the pollen-grains has at its equator three projections, resembling closed bottle-necks with swollen, circular mouths. Very frequently the thin places are disc-like, and may be compared to the glazed port-holes of a ship. It is especially this form which suggests that the outmost layer of the wall is perforated from the beginning. In Umbelliferae, Rosaceae, Papilionaceae, Violets, Rutaceae, Hypericineae, Scrophulariaceae, and other groups of plants, the little circular windows lie hidden in the grooves; in *Cobaea scandens* (217<sup>1</sup>) they are in the "cells" of the honey-comb, and in Onagraceae, *e.g.* Enchanter's Nightshade (*Circæa*), the outer coat is continued as a thin investment over the tops of the projecting warts (fig. 217<sup>5</sup>). The number of windows varies from plant to plant. Cypéraceae have one; Bromeliaceae and the Meadow Saffron, Figs and Brugmansias two; Nettles, Oaks, and Beeches, Evening Primroses and Willow-herbs, and many other plants three; Alders and Birches four to six; Currants eight to twelve; Convolvuluses fifteen to eighteen; Carnations, Oraches, and Mezereons twenty to thirty; and Nyctagineae over thirty.

Having concluded the description of the walls of pollen-grains, the question arises, for what purposes are all these remarkable structures, these grooves and striæ, these chinks and furrows, thorns and spines developed? What is the meaning of the coats of oil and viscin? What of the thin places, and windows, and tiny lids?

Of these the last question is the easiest to answer. As observation shows, pollen-grains swell up with lightning rapidity when they are placed in water. The



protoplasm within, destined for fertilization, takes up water from the environment very quickly and energetically. In consequence it swells rapidly, and must have an inclosing wall which will not impede its rapid stretching. For this purpose the thin places and folds are admirably suited. Through them fluids readily pass to the interior, and simultaneously the grooves (previously folded inwards) become inflated, and the pollen-grains come to occupy two to four times the space they previously did. The thicker portions, saturated with oil, play a purely passive rôle in these events. Water cannot enter by these parts, nor do they stretch with the swelling up inside. Later, when the intine has grown out and assumed the form of a tube, the outer wall is not essentially altered. The thin spots have been ruptured, and where lids are present, they are raised; the protoplast, enveloped in the tube-like intine, vacates the extine by one of the thin spots, much as a germinating embryo does its seed-coat. Just as it is of advantage in germination for the seed-coat to be fixed on the substratum, whilst the young plant gets a good hold of the ground, so here it is of value to the young pollen-tube as it quits the extine of the pollen-grain that the coat should be fixed firmly; for this purpose the various ridges, teeth, and spines possess a high significance, serving as a means of anchoring the pollen-grain whilst the pollen-tube is being formed.

But the most important service rendered by the sculpturings and inequalities of the walls consists in the fact that thereby considerable quantities of pollen-grains are enabled to cohere in crumbling masses to the slits of the opened anthers, and to become attached to insects and other animals visiting the flowers for food. Contrasting with this *clinging pollen* is the already-mentioned *dusty pollen*, with smooth and non-adhesive surface. Dusty pollen does not cohere in clusters, nor does it readily attach itself to foreign bodies. On the other hand, the least disturbance or breath of air carries it away in clouds.

It is sufficiently obvious that globular or ellipsoidal pollen-grains with smooth surfaces will be distributed in the form of dust more readily than grains possessing an angular or crystalline form. The former have a smaller surface of contact than the latter. When the surface is, in addition, variously sculptured and raised into folds and inequalities, the points of contact are of course enormously increased. The little projections of the surfaces of adjacent grains interlock like the wheels of a watch; longer ones become entwined like fingers; thus it comes to pass that hundreds of neighbouring pollen-grains hang together like burs. That such masses will readily attach themselves to the hairs, bristles, probosces, and legs of insects hardly needs further demonstration.

This capacity for clinging is much increased when the surfaces of the grains are saturated with oil. The sticky property of the viscin has been already enlarged upon. We may thus summarize the whole matter in the statement that the crystalline forms, the various sculpturings, spines, and other projections, as well as the presence of oil and viscin on the surface are arrangements in virtue of which the adhesiveness of the pollen-grains is increased.

According as one or other of these arrangements is present or absent we find

every degree of cohesiveness in pollen—dusty, floury, crumbly, clotted, glutinous, waxy. A marked contrast is noticeable between flowers the anthers of which produce dusty, and those which produce coherent pollen. So pronounced is this, that we shall treat of the pollination of these flowers, and in particular of the transmission of the pollen from flower to flower, under separate headings. Here it need only be added that this distinction between dusty and coherent pollen is found not only with isolated pollen-grains but with tetrads. When the stamens of Heaths (*Erica*) are disturbed the pollen escapes in clouds of dust, just as it does from the catkins of the Hazel. This dust, however, consists, not of isolated pollen-cells, but of tetrads. In Azaleas and Rhododendrons, on the other hand, the pollen-tetrads cling together into sticky filaments, just as do the isolated grains of the Evening Primrose and Willow-herb.

Why it is that the pollen is in some cases in tetrads and in others in isolated grains, why its adhesiveness is promoted by such various means as those enumerated, is difficult to say. These differences are perhaps connected with the varying form of the insect-visitors which carry the pollen away, and of the stigmas upon which it is deposited. That the sculpturings protect the pollen against untimely wetting will be shown in the following chapter.

#### PROTECTION OF POLLEN.

The approach to Venice from the mainland is by a long embankment, on either side of which the traveller commands an endless vista of marshes full of reeds and rushes broken here and there by expanses of brackish water—the famous lagoons—which themselves exhibit a luxuriant vegetation consisting principally of Pond-weeds and Naiadaceæ. One plant in particular, the Grass-wrack (*Zostera*), is conspicuous for its abundance in the lagoons, covering, as it does, extensive tracts of the sandy mud at the bottom of the shallow water. The leaves are submerged, ribbon-shaped, and of a brownish-green colour somewhat resembling sea-weed, and, when collected and dried, they are known in commerce by the name of “Sea-grass”, and are used in the packing of glass, and of late years also for stuffing mattresses and cushions. These Grass-wracks, of which there are two known species, differ so greatly from other Phanerogams, not only in appearance, but also in development and in the mode of pollination, that one might almost be induced to assign to them and their immediate allies a special class, were it not that the fact of the existence of numerous intermediate forms and connecting links tells against their isolation.

In the first place, the pollen in *Zostera* does not possess the outer coat which is so characteristic of the cell-membranes of most pollen-cells. Further, from the moment the pollen-cells are set free by the opening of the anthers—an event which occurs under water—they exhibit the form of elongated cylindrical tubes. In the plants most nearly related to the Grass-wracks, namely, the genera *Posidonia* and *Cymodocea*, some species of which grow in brackish and some in salt water, the long hypha-like pollen-cells lie in complicated coils and curves within the anther, and

when they escape from it, and are carried by the water against the long filiform stigmas they adhere to those structures as do the spermatozoids (spermata) to the trichogyne in the Red Sea-weeds (*cf.* pp. 60, 61). The filamentous pollen of *Halophila* is even divided by transverse septa into several chambers, or, more accurately, the pollen-cells are aggregated into long strings. The pollen-cells are intercepted under water by the filiform stigmas and grow down them into the ovaries. In the different species of *Naias* as also in those of *Zannichellia* the pollen-cells are spherical or ellipsoidal in shape so long as they are inclosed in the anther, but when the anther opens they assume the form of tubes, and are wafted about by the water until they reach the stigmas. The stigma in *Zannichellia* is triangular and comparatively large, and owing to the fact that three or four such stigmas have their edges in contact, a sort of funnel is formed, which serves to collect the pollen-cells as they float about.

The plants above referred to, about fifty species in all, were classed together by the older botanists under the name of *Naiadaceæ*, but are now grouped into the families of the Potamogetonaceæ, Naiadaceæ, and Hydrocharidaceæ. They are all aquatic plants, but it would be erroneous to suppose that all the members of these groups possess the same kind of pollen as is exhibited by the Grass-wracks, and the various species of *Halophila*, *Posidonia*, *Cymodocea*, *Naias*, and *Zannichellia*, that is to say, a filamentous pollen destitute of external coat which is conveyed to its destination by currents of water. On the contrary, thousands of aquatic plants discharge their pollen above the surface of the water and not beneath it. The pollen-cells are spherical or ellipsoidal, have a distinct external coat, and are transported to the stigmas not by flowing water but by the wind or by insects. This is the case even in plants whose leafy parts remain under water throughout their lives. *Aldrovandia*, *Hottonia*, and *Utricularia*, many Pond-weeds (*Potamogeton*) and Water-crowfoots (*Ranunculus*), not to mention many others, always raise their flowers above the surface of the water, so that the pollen may escape into the air and be blown or otherwise conveyed from one flower to another. I have observed that even in the case of the various species of Water-starwort (*Callitriche*), which were formerly said to accomplish their fertilization under water, the anthers open only in the air, and that the staminal filaments grow in length according to circumstances until the anthers project above the surface. If they fail to do so, then the anthers of the flowers in question do not open at all; the spherical pollen remains inclosed and decays, together with the anther and its filament, beneath the water. The far-famed *Vallisneria* (see vol. i. p. 667), too, to which we shall return again later on, only emits the pollen from its anthers into the air. The stamiferous buds, it is true, develop under water; but they detach themselves from the axis of the inflorescence in the form of closed bladders, and do not open until they reach the surface. The stamens then project out of the floating flowers into the air, the anthers burst, and the pollen is set free (*cf.* fig. 227). If the buds are kept submerged artificially, neither they nor the anthers open, but they decay, and the pollen perishes under the water. And, as in the case of these aquatic



plants, so also in that of the multitude of plants which germinate and flower on dry land, if the pollen happens to fall into the water or is purposely kept immersed, it is destroyed.

It is thus the fact that the pollen of Phanerogams, with the exception of about fifty species, of which the Grass-wracks may be taken to be the type, is injured by prolonged immersion or subaqueous transport. This obviously suggests an inquiry as to the reason of the hurtful action of water upon cells which require an especial abundance of liquid materials for the development of the pollen-tubes. There is, however, a great difference between the absorption of pure water and the absorption of the liquid substances yielded by stigmas. A pollen-cell deposited upon a stigma gradually takes up the liquids there available, and the pollen-tube pushes out comparatively slowly. If, on the other hand, the pollen-cell is put into water, or is in nature so wetted by rain or dew as to be practically immersed in a water-bath, absorption of water takes place almost instantaneously; the intine is pushed out wherever no resistance is offered by the extine, and in a moment the pollen-cell swells up. Such a process cannot properly be called a development of the pollen-tube. No real growth can take place in so short a time, and what has occurred is simply an expansion of the intine and a smoothing out of the folds which have hitherto lain tucked in. Frequently, indeed, the limits of elasticity are exceeded; the projecting part of the intine bursts, and the spermatoplasm flows out into the water in the form of a finely granulated, slimy mass. In that event the pollen-cell is destroyed, and comes to nothing. But even if the intine does not burst, the pollen undergoes such complete alteration through the rapid absorption of water that its protoplasm loses the power of fertilization. It seems as if the protoplasts inclosed in pollen-cells, subjected to prolonged immersion, were literally drowned. Thus much is certain, that the immense majority of pollen-cells perish under water, and that even if wetted they incur great risk of destruction. This danger, which may be of daily occurrence in case of rain or heavy dew, has to be avoided. In order to preserve the pollen fit for use it must be secured by protective apparatus against the injurious effects of moisture, especially against atmospheric deposits; it must be able to develop under conditions from which this factor—in so far as it is harmful—is, generally speaking, excluded.

In regions where there is a regular alternation of rainy and rainless seasons—in the llanos of Venezuela, the Brazilian campos, the dry districts of India and the Soudan, above all, in the parts of Australia to the south of the tropic where the rainfall is limited to the winter and afterwards ceases for months—the climate itself indirectly affords security to the pollen against risk from water; or, in other words, any apparatus to protect from rain the pollen of plants which flower in rainless seasons would be superfluous. The trees which wave above the grass of the wonderful savannahs of Australia, as also the numerous dry and rigid shrubs which belong to the adjacent "scrub", do not flower until the rainy season is over, when the flowers do not run any risk of being drenched with rain. In the absence of the danger the necessity for any direct means of defence against it also





ALPINE RHODODENDRONS AND MOUNTAIN PINES (TYROL).





disappears, and in Australia the numerous Mimoseæ and Myrtaceæ and the Proteaceæ, which constitute the principal part of the dense copses just referred to, are accordingly destitute of any contrivance capable of acting as a protection to the pollen. These plants preserve their rigid character even during the flowering season; the filaments bearing the anthers project in large numbers far beyond the small floral envelopes in the Acacias and in the innumerable species of *Callistemon*, *Melaleuca*, *Eucalyptus*, *Calothamnus*, and *Metrosideros*, and the styliform prolongations of the ovaries in Proteaceæ, on the top of which the pollen is deposited when set free from the anthers, spring up and stretch out unprotected far beyond the restricted perianth.

Flowers which inhabit a region where moisture is deposited from the atmosphere in greatest quantity in the flowering season exhibit an entirely different form. In the mountains of Central and Southern Europe, where this coincidence occurs, the plants whilst in flower must be prepared for daily showers. In addition every plant drips with dew in the early morning, and drops of water are deposited on leaves and flowers in the course of the day by the mists as they roll by. It must often happen that the pollen remains for days together hanging to the opened anthers before it is carried away by bees or butterflies to the stigmas of other flowers. Here if anywhere is an instance of the necessity of ample shelter for the pollen. Examine the plants composing the smaller brushwood of such a region, and you will find how great a contrast they afford to the plants of the thickets of Australia. The flowers of the Heather (*Calluna vulgaris*), and of the Bilberry, Bog Whortleberry, and Cowberry (*Vaccinium Myrtillus*, *V. uliginosum*, *V. Vitis-Idæa*) have bell- or cup-shaped corollas which hang down from curved stalks with the mouths of the flowers towards the earth, and so cover the pollen-laden anthers. Similarly, we find the Alpine Rhododendrons ("Alpine Roses"), which clothe the mountain sides, with flowers inclined at a right angle to the erect stalks so that the anthers are perfectly sheltered (*cf.* Plate X., after a drawing by E. Heyn).

All the many contrivances whereby pollen is directly protected from wet are of the same nature as the above, the method of protection being by some such roofing in or envelopment of the anthers. That these adaptations should exhibit so much variety in detail in spite of the uniformity of their object is due to the condition that the envelopment must itself not be carried too far. On no account must the dissemination of the pollen or its transport by wind or insects to the stigmas of other flowers be hindered; nay, the very same parts of a flower which shelter the pollen from rain frequently have the additional function of assisting the dispersion of the pollen when the rain is over.

In the enumeration of arrangements for warding off injury to pollen from wetting, the various coverings and protections are described as equally effective for rain as for dew. But this, of course, is not for the same reason. A roof protects structures from rain by intercepting the drops, and from being bedewed since it diminishes radiation from the bodies beneath and thus keeps them at a

higher temperature than would otherwise have been the case. This explanation must be borne in mind.

We find, therefore, an amount of variety in the forms of safeguard against wet corresponding to the multiplicity of the adaptations which subserve the purpose of pollen-transport by the wind or by butterflies, bees, beetles, or flies, as the case may be. The means of protection are diversified also according to whether the cover is placed immediately over the pollen or over an entire group of flowers, whether it shelters the newly-opened, pollen-laden anthers or that part of the flower whereon pollen liberated from the anthers is temporarily deposited; and again they vary according as it is the anther-walls, stigmas, petals, involucre, or foliage-leaves which have to serve as roof to the pollen. The Lime-tree affords an instance of the last-mentioned arrangement, its flowers being invariably so placed that at the time when pollen is yielded by the anthers they are covered by the broad, flat foliage-leaves. However sharp the showers to which a Lime-tree is subjected the rain-drops roll off the blades of the leaves, and it is only by exception that any one of the many flowers stationed beneath them is wetted. The same provision is met with in a few species of *Daphne* (e.g. *D. Laureola* and *D. Philippi*), in several Malvaceæ (e.g. *Althæa pallida* and *A. rosea*), and in the *Impatiens Nolitangere*, a plant which possesses other remarkable features and will be the subject of further discussion by and by (*cf.* fig. 220<sup>1</sup>). In *Impatiens* the flower-buds are held by their delicate stalks above the surfaces of the leaves from whose axils they spring, and the leaves are at first folded upwards like erect troughs. Subsequently, when the buds get bigger and their stalks longer, the latter slip down to one side of the leaves and hide beneath them, whilst the leaf-margins still continue to be curved upward. The leaf then flattens itself out and fixes the drooping flower-stalk by means of one of the lobes of its heart-shaped base, and thus indirectly keeps the suspended bud in position, so that when later on the bud and its anthers open, which they do simultaneously, they are roofed over by a smooth lamina, off which the rain-drops roll without ever wetting the flowers or their pollen (fig. 220<sup>1</sup>).

In many Aroidæ the spadix is completely covered by the large sheathing leaf or spathe at the time when the anthers burst, as, for instance, in the curious Japanese *Arisema ringens*, where the spathe curves over the inflorescence like a Phrygian cap, and in *Ariopsis peltata*, where the spadix is protected from rain and dew by a sheathing leaf resembling a boat with the keel uppermost (*cf.* fig. 221<sup>1</sup>). *Genetyllis tulipifera*, a shrub belonging to the Myrtaceæ, bears at the ends of slender, woody twigs inflorescences which at first sight might be taken to be pendent tulips. On closer inspection it appears that the large white leaves with red veins which recall the leaves of the tulip perianth are involucre bracts which cover the closely-crowded flowers and shield them from the rain. Similarly in the case of the Banana and its allies (*Musa*, *Ravenala*) the flowers are covered over when the pollen is mature by large involucre sheaths which subsequently, after the pollen has been used up and there is no longer any need



for protection, detach themselves and drop to the ground. Fig. 220<sup>2</sup> shows the male flowers of the diœcious Sea-Buckthorn (*Hippophae rhamnoides*), which are arranged in spikes and are seated in the axils of scaly bracts at the bases of the young lateral shoots. In each flower are four anthers which discharge their abundant powdery pollen whilst the flower is still closed like a bud and has the appearance of a little bladder (fig. 220<sup>3</sup>). This pollen is of an orange colour, and drops to the bottom of the flower, where it remains (figs. 220<sup>4</sup> and 220<sup>5</sup>) awaiting a dry wind to transport it to the stigmas of the female flowers growing on other plants often at a considerable distance. Several days may go by before



Fig. 220.—Protection of Pollen from Wet.

<sup>1</sup> *Impatiens Nolitangere*.    <sup>2-5</sup> *Hippophae rhamnoides*.    <sup>6</sup> *Convallaria majalis*.    <sup>7</sup> *Euphrasia officinalis*.    <sup>8</sup> *Iris sibirica*.  
<sup>1</sup>, <sup>2</sup>, <sup>6</sup>, <sup>7</sup>, <sup>8</sup> natural size; <sup>3</sup>, <sup>4</sup>, <sup>5</sup> slightly magnified.

this kind of wind sets in, and meanwhile there is the danger of the store of pollen being soaked by rain or dew and rendered unfit for dispersion. To obviate this risk the pair of curved perianth leaves, which have their concave surfaces turned towards one another, and form, as has been already mentioned, a kind of bladder inclosing the anthers and pollen, dehisce at the sides only. Thus two opposite gaps (figs. 220<sup>4</sup> and 220<sup>5</sup>) are produced, whilst at the top the two valves remain joined together and form an arch completely sheltering the mass of fallen pollen from atmospheric deposits. When the needful wind arises it blows the pollen out through the chinks in the bladder and conveys it to the stigmas of other plants of the same species.

Plants of the Globe-flower (*Trollius*) genus, whose species grow in the Arctic regions in damp situations and also further south in mountainous districts of the

Old World, are daily exposed to rain or heavy dew. Nevertheless their pollen is never wetted, the anthers being completely shut in by the perianth-leaves, which are spirally inserted on the receptacle and closely furled one upon another. These flowers have a ring of stalked nectaries round the stamens, and insects which visit them for the sake of the honey are obliged to break through the roof formed by the overlapping perianth-leaves in order to reach the inside of the flower. The pliability of these leaves enables bees by their weight to effect an entrance, whilst falling drops of rain cannot penetrate, but roll off the flower.



Fig. 221.—Protection of Pollen from Wet.

<sup>1</sup> *Ariopsis peltata*. <sup>2</sup> Flower of *Trollius europæus*. <sup>3</sup> The same with some of the floral-leaves removed. <sup>4</sup> *Digitalis lutescens*.  
<sup>5</sup> A single flower of *Digitalis lutescens* in longitudinal section. <sup>6</sup> *Aretia glacialis*. <sup>7</sup> Single flower of *Aretia glacialis* in longitudinal section (magnified).

Also in *Corydalis*, *Calceolarias*, Toad-Flax and Snap-dragon (*Corydalis*, *Calceolaria*, *Linaria*, *Antirrhinum*) the corolla forms a closed envelope round the anthers; and again in papilionaceous flowers the pollen is, up to the moment of an insect's visit, hidden in the cavity formed by the two petals of the keel.

The majority of lipped flowers—Butterwort, Yellow-rattle, Cow-wheat, and Eye-bright (*Pinguicula*, *Rhinanthus*, *Melampyrum*, *Euphrasia*, cf. fig. 220<sup>7</sup>)—as also the Violet (*Viola*), Monkshood (*Aconitum*), and innumerable other plants whose flowers open laterally, do not regularly inclose the pollen, but protect it against rain or dew by means of an arched portion of the flower which forms a roof over it. In *Acanthus* the flowers are inclined laterally, and, though

resembling bi-labiate flowers in general appearance, possess no prominent upper lip, the protection of the pollen being effected by a sepal which stretches out at the place where the upper lip would be. A curious arrangement for the protection of pollen by sepals may be observed in the inflorescence of *Hydrangea quercifolia* (fig. 222<sup>8</sup>), a native of Florida allied to the Hortensias. The flowers of this plant grow in handsome bunches, and are of two kinds: the one kind includes stamens and pistil, but only a very small, greenish perianth incapable of shielding the pollen of the adjoining stamens from rain or dew; the other has neither stamens nor pistil, but has very large, white, expanded sepals which are arranged so as to constitute with their erect stalks a sort of umbrella. The flowers of the latter type are developed on the outermost and uppermost branches of the inflorescence, and are always in a position to stop the rain from falling upon the umbels of small pollen-bearing flowers which are situated underneath them.

In rare cases the stigmas act as pollen-protectors. The most striking instance is that of the genus *Iris*. The stigmas in the *Iris* are petaloid, and consist of three foliaceous structures gently curved outwards, and each terminating in a pair of dentate apices (cf. fig. 220<sup>8</sup>). The upper surfaces of these foliaceous stigmas are convex and usually somewhat keeled along the middle line, the under surfaces are concave. Beneath each stigma one finds a pollen-laden anther nestling close against the concave surface, and so perfectly concealed that it is impossible that it should ever be reached by a drop of water however heavy the rain.

Flowers of the form called "hypocrateriform" by botanists are adapted to the protection of their pollen on an essentially different principle. The species of *Phlox* and *Daphne* included in this category, the delicate species of Primulacæ belonging to the genera *Androsace* and *Aretia*, which dwell amid mountain-mists, and the pretty, erect-flowered Primulas (e.g. *Primula farinosa*, *P. denticulata*, *P. Cashmiriana*), all bear flowers which are not roofed in, but have the mouths of their corollas open to the sky, the tubular part of the corolla passing abruptly into an expanded limb (cf. figs. 221<sup>6</sup> and 221<sup>7</sup>), so that drops of rain or dew collect on the limb surrounding the mouth of the tube. Here it seems inevitable that some drops of water should reach the anthers inserted in the tube. Yet, as a matter of fact, the pollen is kept dry. For, at the place where the tube passes into the limb of the corolla it is abruptly contracted, besides being often also studded with callosities, in consequence of which the opening is so narrowed that, although insects with fine probosces gain access to suck the honey in the flower, any rain-drops that may happen to be lying upon the limb do not gain admission because the air cannot escape from the tube. If flowers of *Aretia glacialis* (fig. 221<sup>6</sup>), a plant growing on the moraines of glaciers, are examined after a shower, it is found that every one has a drop resting upon it which slightly compresses the air in the narrow tube of the corolla, but cannot reach the pollen upon the anthers lower down the tube. A subsequent shake or puff



of wind causes the drops to roll off the limb of the corolla, or else they are got rid of by evaporation; in either case, the flower becomes once more accessible to insects.

In none of the instances hitherto described does any change take place in the relative positions of the foliage-leaves, petals, or petaloid stigmas, whereby the pollen shall be the better protected. On the other hand, there is a long list of plants wherein the protection of the pollen is effected exclusively by means of changes in the position of some one or other of the leaves in question. This occurs especially in all those species which, like the forms last mentioned,



Fig. 222.—Protection of Pollen from Rain.

<sup>1</sup> Flower of *Eschscholtzia Californica* opened in the sunshine. <sup>2</sup> The same closed in wet weather. <sup>3</sup> Floral capitulum of *Hieracium Pilosella*, closed. <sup>4</sup> Single flower of the same plant. <sup>5</sup> Capitulum of the same, open. <sup>6</sup> Longitudinal section through a closed capitulum of *Catananche caerulea*. <sup>7</sup> Single flower taken from the capitulum in the last stage of flowering. <sup>8</sup> Portion of inflorescence of *Hydrangea quercifolia*. <sup>9</sup> Young closed flower of *Eranthis hiemalis*. <sup>10</sup> Old closed flower of the same.

have the mouths of their flowers exposed to the incidence of rain, or unshielded, so that radiation is not diminished and dew is formed, but, unlike them, exhibit no sufficient constriction of the tubular part of the corolla to prevent drops of water from falling into the flowers. Such unconstricted, cup-shaped, urceolate, infundibular, or tubular flowers would, if upright, constitute regular rain-collectors, and the water would at once saturate the pollen within the flowers. If flowers of the kind close up temporarily and keep their petals or involucral leaves arched over the interior so long as there is any risk of water collecting there, the requisite security from inundation is attained by very simple means. As a matter of fact, protection of pollen is effected in numerous cases by the closing of flowers. Examples of this are afforded by the flowers of Meadow Saffron, Sternbergias, and Crocuses (*Colchicum*, *Sternbergia*, *Crocus*, cf. fig. 223),

which lift the cup-shaped limbs of their corollas above the ground in the spring or late autumn, the Gentians of Alpine meadows and their allies of the Centaury genus (*Erythraea*), a host of Bell-flowers with erect blossoms (*Campanula glomerata*, *C. spicata*, *C. Trachelium*, *Specularia Speculum*, &c.), the Peonies, Roses, Flaxes, Opuntias, Mammillarias and Mesembryanthemums, numerous species of the Star of Bethlehem, and Thorn-apple genera (e.g. *Ornithogalum umbellatum*, *Mandragora vernalis*, *Datura Stramonium*). The floating flowers of the Water-lily (*Nymphaea*), and the large flowers which are borne



Fig. 223.—Protection of Pollen.

Flowers of *Crocus multifidus*. On the right, flowers open in the sunshine; on the left, flowers closed at night or in wet weather. One of the three closed flowers has some of its perianth-leaves removed.

on the branches of Magnolias also belong to this group of forms. Throughout the day when the sun is shining the floral cups or funnels of these plants are wide open and often even expanded into stars, whilst swarms of insects hover round them; but at dusk when the dew "falls" the petals close up again and overlap one another so as to form a case (*cf.* fig. 223) upon which any amount of dew may be deposited without affecting the interior of the cup. In damp or rainy weather these flowers do not as a rule open. Thus the period of their being closed coincides with a time when most honey-seeking insects are absent, having either gone to rest for the night, or retired to their hiding-places for shelter from the wet.

It is a very interesting phenomenon that petals which close over the anthers



in the evening grow much larger in the course of the flowering period. In many species they become double as long as they were at the moment the flower first opened. The enlargement of the petals takes place *pari passu* with certain processes in the development of the anthers to be protected. Some Ranunculaceæ with erect flowers—e.g. the Hepatica (*Anemone Hepatica*) and Winter Aconite (*Eranthis*, cf. figs. 222<sup>9</sup> and 222<sup>10</sup>)—have their pistils surrounded by a crowd of stamens, and these again encircled by concave perianth leaves (petaloid sepals) which are wide open by day but closed at sunset, forming a dome over the stamens. The anthers of these plants do not open simultaneously, but only by degrees. The pollen on the outermost anthers nearest to the sepals is set free first of all, and this happens at a time when the filaments bearing those anthers are still short. It is obvious that comparatively short sepals suffice to shelter these stamens. Gradually, however, the anthers nearer the middle of the flower open; their filaments elongate, and the sepals would now be no longer of sufficient size to form a dome over all the pollen-laden anthers at night time. They accordingly grow in length day by day, until the anthers next to the carpels yield up their pollen. In the case of *Eranthis* the sepals lengthen in this way from 11 to 22 millimetres (cf. figs. 222<sup>9</sup> and 222<sup>10</sup>), and in that of *Anemone Hepatica* from 6 to 13 millimetres; that is to say, they actually double their original length.

A curious instance of the closing of petals is that of *Eschscholtzia Californica* (cf. figs. 222<sup>1</sup> and 222<sup>2</sup>). By day the four golden-yellow petals are expanded, the pollen falls from the stamens, which grow in a bunch in the middle of the flower, on to the concave petals, and rests on them in a floury layer as much as 1 millimetre in depth. When evening comes the anthers in the centre, having already lost their pollen, are left unprotected, but each petal furls itself up longitudinally in the prettiest manner conceivable, and thus the fallen pollen is sheltered under four little tents.

The flowers composing the capitula of the Dandelion (*Taraxacum*), Lettuce (*Lactuca*), Chicory (*Cichorium*), Nipple-wort (*Lapsana*), and many other Composites, of which we may here select the Mouse-ear Hawkweed (*Hieracium Pilosella* (fig. 222) as type, have tubular bases, but above are produced unilaterally into a strap-shaped structure to which the term ligule is applied. From the bottom of each ligulate flower spring five stamens whose anthers are connate into a tube. This tube is early filled with pollen discharged introrsely, i.e. towards the centre of the flower through longitudinal slits in the anthers. The style is embedded in the tube, and as soon as the pollen is liberated it elongates, and, acting like a chimney-sweep's brush, pushes up the pollen which fills the anther-tube until it rests above the opening at the top. The pollen resting on the top of the style is brushed off by insects when they settle upon the capitula. But it is not certain that insects will make their appearance within a few hours of the extrusion of the pollen, and even if they do they only brush lightly over the flowers, and are sure to leave some of the pollen behind, and this pollen is



then reserved for another destiny which we shall have to consider more carefully later on. In any case the pollen adherent to the projecting end of the style, near the mouth of the tube composed of the connate anthers, must be protected before nightfall, when there will be condensation of dew, or in case of rain being imminent. This protection is, in fact, afforded to each floret by the ligule of the adjoining corolla, which stretches out laterally and constitutes an umbrella. In the Hawkweeds (*Hieracium*) the ligule bends so as to form a covering over the pollen to be protected (*cf.* figs. 222<sup>3</sup> and 222<sup>5</sup>). In *Catananche*, another Composite, each ligule is spread out flat whilst the sun shines, but in the evening becomes concave and at the same time arches over the pollen belonging to its own flower (fig. 222<sup>6</sup>). We cannot here go into all the differences in detail which occur in connection with this form of adaptation. We must not, however, overlook the fact that in these Composites the ligules of the peripheral florets of a capitulum are always much longer than those of the central florets, and that the pollen of the latter shares therefore the protection from wet afforded by the bending over of the outer ligules. We do not mean to say that the short ligules in the middle of the capitulum are not required to take any part at all in sheltering the pollen. In most instances they, too, stand up and curve over inwards, and act in conjunction with the longer outer ones in preventing the entrance of water. The adaptation of the flowers of *Catananche* is carried so far that the long ligules of the peripheral florets cease to bend inwards when there is no longer any pollen to protect in those florets—that is to say, when the pollen has been brushed off and the florets have entered into their last stage of development (*cf.* fig. 222<sup>7</sup>). The short ligulate florets in the central part of the capitulum must then of course see to the protection of their pollen themselves. This is the reason why one sees only the central ligules of old heads of *Catananche* arched inwards, whilst those near the margin remain motionless and stand out in rays during the dewy night just as they do under the noontide sun.

The mechanism for the protection of the pollen is well worthy of notice in those Composites also in which the central florets of the capitula are all tubular and the peripheral florets all ligulate, and in those where the tubular florets are crowded together on a round disc and encompassed by an involucre of stiff leaves which resemble petals. The Marigold (*Calendula*) may be taken as type of the first group, and the Carline Thistle (*Carlina acaulis*) as type of the second (fig. 224). In these plants the style grows and pushes the pollen out at the top of the tubular florets, just as in the case of the ligulate flowers above described it was pushed up through the hollow cylinder formed by the connate anthers, and above each floret a little lump of pollen is seen resting upon the free end of the style. These tubular florets are, however, incapable of securing their pollen against bad weather, and a division of labour is therefore in some degree instituted within the limits of each capitulum, the ligulate florets or radiating marginal bracts, as the case may be, which produce no pollen, being turned to account for the purpose of sheltering the pollen-bearing florets of the centre. In fine

weather the ligulate florets and bracts stand out in rays from the periphery of the capitulum, but in bad weather and at night they are raised and actually bent over the central tubular florets. They are either disposed so as to form together a hollow cone over these florets, or else they overlap one another like the tiles on a roof; often, too, they are twisted together in apparent disorder into a tuft, but they are always so arranged as to afford complete shelter to the central florets and to the pollen exposed by them.

It is a remarkable fact that the length of these incurving rays stands in a definite relation to the diameter of the capitulum. Heads with large discs and great numbers of tubular florets have relatively long marginal rays, those with small discs and few tubular florets have relatively short rays. Moreover, at first when the florets in the middle of the disc are still closed, and only the tubular florets set near the margin have extruded their pollen, the ligulate florets of the ray and the radiating bracts are still short because they only have to shelter their nearest neighbours; but as soon as the flowers in the middle of the disc open, the peripheral florets lengthen so as to be able to cover them also. Thus the roof here actually grows in proportion to the dimensions of the surface requiring shelter.

The changes affecting the position of petals, ligulate florets, and bracts, which have been briefly described and which are classed together under the name of closing movements, take place in most plants in from thirty to fifty minutes, but in a few cases they are much more rapid. Sometimes the process of closing is completed in the course of a few minutes. With Alpine plants it may happen that the flowers shut and open several times within an hour. The warmth imparted by a casual ray of sunshine is sufficient to cause the flowers of *Gentiana nivalis* to spread out their deep-blue petals, but no sooner does the sun disappear behind a cloud than the petals wind themselves round one another in a spiral and close up, forming a hollow cone. If the sun comes out again the corolla is once more open in the course of a few minutes.

In plants with funnel-shaped, tubular, or bowl-shaped corollas, as, for example, the Thorn-apple, Gentians, and the Venus' Looking-Glass (*Datura*, *Gentiana*, *Specularia*), the phenomenon of closing is attended by a complex folding, bending, and twisting of the petals; but as a rule the position assumed by the petals on such occasions is the same as that which they previously exhibited in the bud. Generally speaking, most flowers and heads of flowers when closed at night have the same appearance as they had in the bud state.

For the proximate cause of the movements of closing we must undoubtedly look to alterations in the tension of the layers of tissue involved in the operation. These alterations are due chiefly to variations of heat and light. Fluctuations in the degree of moisture of the air may also partly contribute to the result. In the Carlina Thistle (*Carlina acaulis*), indeed, the opening and closing of the heads depends solely on this condition, and temperature is only a factor inasmuch as the relative moisture of the air is generally diminished as the heat increases in the parts of the world where the plant grows. Owing to this property of



*Carlina acaulis*, its large heads of flowers are used as hygrometers and weather-glasses. When the dry bracts surrounding the tubular florets of the capitulum stand out in rays dry weather and a clear sky are indicated, but when the hygroscopic bracts become erect and subsequently converge, so as to form a hollow cone, wet and cloudy weather is anticipated (*cf.* fig. 224). The significance of these movements of the radiating bracts or involucral leaves to the plant itself is as follows. By day when the air is warm and dry the rays have an outward curve and are spread out widely so as to turn their inner surfaces, which are silvery white, to the sky, and they glisten so brightly in the sunlight that they are visible from a great distance. They thus act as a means of alluring insects



Fig. 224.—Protection of Pollen.

Capitula of the Carline Thistle (*Carlina acaulis*), the one on the right open as in the sunshine, that on the left closed as at night or in bad weather.

to the inconspicuous tubular florets of the disc, and these visitors whilst sucking the honey also load themselves with the exposed pollen and subsequently convey it to other flowers. A large number of humble-bees alight on the open capitula of the Carline Thistle, suck the honey from the florets, and at the same time remove the pollen. If at that moment there were to be a sudden shower of rain the florets of the disc would inevitably be wetted and the pollen ruined. But owing to their hygroscopic sensitiveness the rays rear themselves up on occasion of even a slight increase of moisture in the air such as precedes rain, and, bending inwards, unite into a compact tent, off which the drops of rain roll without being able to do any mischief.

Alterations in the form and position of certain tissues of the stamens due to the taking-in and giving-out of water also afford a means of protection for pollen against wet in the case of Plane Trees, and of many Conifers, Yews, and Junipers



in particular. The pollen-cases are in these plants borne on squamous or peltate stalks, which are attached to an axis in a manner similar to the scales of a fir-cone. They also possess in common with the scales of a cone the property of closing and bringing their margins into contact when they are moistened, whereas when quite dry they stand away from one another, leaving wide intervening gaps (*cf.* figs. 226<sup>15</sup> and 226<sup>16</sup> with figs. 226<sup>17</sup> and 226<sup>18</sup>). The pollen-dust which is developed in little spherical pollen-cases on the inner faces of the scales, is very liable to be shaken out of these gaping interspaces, but such an occurrence, as will be presently more fully explained, is only advantageous to the plant if dry weather prevails. In damp weather, and especially during rain, such escape would be equivalent to destruction of the pollen. To avoid this risk the gaps close up, an operation which is effected by the scales absorbing moisture and swelling until their edges are in contact, so that the little pollen-cases attached to their inner surfaces are covered up.

In the flowers hitherto described the parts adapted to the protection of the pollen from wind and wet are all leaf-structures or scaly or peltate outgrowths from the connectives of the stamens, and the adapted structure is bent or hollowed out, expanded or folded, as the case may be. Another group of floral forms, scarcely less considerable than the foregoing in point of numbers, secures this protection in a still simpler manner by bendings of the stalks and stem which convert bowl and cup-shaped flowers into pendulous bells. Usually the inflection occurs shortly before the blossoming of the flower, and then the flower retains the drooping position so long as its pollen is in need of protection. Many Campanulas (e.g. *Campanula barbata*, *C. persicifolia*, *C. pusilla*), Solanaceæ and Scrophularineæ (e.g. *Atropa*, *Brugmansia*, *Cestrum*, *Physalis*, *Scopolia*, *Digitalis*), Primulaceæ and Boragineæ (e.g. *Cortusa*, *Lysimachia ciliata*, *Soldanella*, *Mertensia*, *Pulmonaria*), Alpine-roses, Winter-greens and Whortleberries (*Rhododendron*, *Moneses*, *Vaccinium*), Ranunculaceæ and Dryadeæ (e.g. *Aquilegia*, *Clematis integrifolia*, *Geum rivale*), and many Liliaceous plants (e.g. *Fritillaria*, *Galanthus*, *Leucojum*, *Convallaria*) may be seen with their flower-buds supported on erect stalks and turned to the sky so long as they are closed. But before the flower is quite open the stalk curves downward, and the mouth of the flower is thus directed more or less towards the earth. No sooner has the flowering period expired, and with it the necessity for shielding the anthers concealed in the interior of the flower, than the stalks, in most instances (e.g. *Digitalis*, *Soldanella*, *Moneses*, *Fritillaria*, *Clematis integrifolia*, *Geum rivale*), straighten out again, and the fruit developed from the flower—especially if a dry fruit—is once more borne at the end of an erect stalk. The phenomenon is illustrated in figs. 221<sup>4</sup> and 221<sup>5</sup>. It is common to hundreds of plants belonging to most widely different families, and exhibits a great variety of modifications. The limits of this work forbid our discussing all these secondary forms of adaptation, which vary partly according to the structure of the stem and flower-stalks, partly according to the form and disposition of the leaves, petals, and stamens. We can only give a brief account of some of the most striking cases.

If the filaments supporting the anthers charged with pollen are small and short, the perianth, which in the inverted flower constitutes their protective cover, is also of small size, as may be seen, for instance, in the case of the Lily of the Valley (*Convallaria majalis*, cf. fig. 220<sup>6</sup>). A much longer envelope is assigned, on the other hand, to stamens with long filiform filaments. Flowers of the kind possessing large petals but seldom need to be completely pendulous in order to shelter their pollen, it is usually sufficient for them to nod, *i.e.* to droop a little to one side. Thus, for example, the stalks of *Lilium candidum* bend in the flowering season only just enough to incline the mouths of the flowers in a lateral direction. Usually the form of the protective cover is such that the rain can trickle off it in drops. A contrivance far less common is for the petals covering the anthers to form a receptacle out of which the water is periodically emptied. An instance of this is afforded by the South African *Sparmannia* (*Sparmannia Africana*). The flower-buds are grouped together in umbels, and are borne on stalks, which are curved in a semicircle outwards and downwards away from the main axis, so that the flowers are inverted and their anthers are turned towards the ground and covered over by the petals. When the flower is open, however, the petals are not simply spread out like an umbrella, but are slightly tilted back, *i.e.* upwards. The margins of the petals overlap one another, and their outer surfaces, which, in consequence of the inverted position of the flower are uppermost, thus form a basin open to the sky. When it rains this basin placed above the anthers fills with water, thus adding to the weight borne by the stalk, and as drop after drop increases the strain upon the latter a point is at length reached when the basin tips over, letting the water flow over its edge without wetting the cluster of stamens suspended beneath it. This mechanism preserves the pollen clinging to the dehiscent anthers of *Sparmannia* from rain and dew in spite of their apparent exposure, which to a hasty observer seems to render it inevitable that the stamens should be wetted.

In some plants whose flowers are arranged in racemes a process of inflection takes place before the flowers open, which does not affect the pedicels themselves but the axis from which they spring, the result being that the entire racemes or spikes become pendent. All the flowers are then inverted, and the petals act as a roof in sheltering the pollen adhering to the anthers. This is the case in the Cherry Laurel (*Prunus Laurocerasus*), the Bird Cherry (*Prunus Padus*), the Barberry (*Berberis*), and *Mahonia*. In the Walnut, the Birch, the Hazel, the Alder, and the Poplar (*Juglans*, *Betula*, *Corylus*, *Alnus*, *Populus*) also, the rachis of the spike changes its position shortly before the dehiscence of the anthers thus providing a shelter for the pollen as it becomes free. The male flowers of these plants whilst in the bud condition are crowded closely together, and form a stiff erect cylindrical spike. But before the flowers open the rachis of the spike grows in length slightly and becomes pendent, whilst the flowers it bears are consequently separated a little from one another and become inverted, so that the floral envelopes, which are composed of little scales and perianth-leaves, are uppermost

and the anthers below them (see fig. vol. i. p. 742). Whilst thus suspended beneath the scales the anthers open and the pollen rolls out. It is not, however, immediately blown away, but falls vertically and collects first of all in trough-like depressions which occur on the external surfaces of the separate flowers. Here it remains until there is dry weather and a puff of wind blows it away to the stigmatic flowers, this being accomplished in a manner that will receive closer consideration later on. Up to this moment its resting-place is sheltered from rain and dew by the flowers situated above it on the same spike, and the appendages of each flower thus constitute, on the one hand, a receptacle for the pollen of the higher flowers, and on the other, a roof over the pollen which has fallen upon the grooved backs of the lower flowers, as is shown in the illustration representing the flowers of the Walnut already referred to.

A special interest attaches to those flowers and inflorescences which assume periodically an inverted position and whose stalks possess the faculty of bending, stretching, or turning concomitantly with the alternations of day and night, and of fine and wet weather. Such plants might quite properly be described as weather-cocks. They include forms belonging to most widely different families, but possessing the common attributes—first, that their flowers or inflorescences are borne on comparatively long stalks, and secondly, that they offer their honey and pollen to the flying insects which visit them in shallow cups or flat saucers, or even on plane discs. In the daytime in fine weather when flowers and inflorescences of this kind straighten out and turn their open surfaces towards the sun, they are plentifully visited by such insects as refuse to enter pendent bells and tubes from underneath, and only alight from above on wide, open, and easily accessible flowers, and thus is effected the important function of pollen-dispersion. On the other hand, by becoming pendent at night and in rainy weather—*i.e.* at a time when insects are not commonly on the wing—they ensure security for their pollen and honey against wet. Hence the periodic movement of the axis appears to achieve a double advantage.

In many Campanulaceæ and Geraniaceæ it is the stalks of individual flowers that bend. The widely-distributed species, *Campanula patula* and *Geranium Robertianum* have been selected from the list of those orders for illustration (*cf.* figs. 225<sup>1</sup> and 225<sup>3</sup> with figs. 225<sup>2</sup> and 225<sup>4</sup>). The same phenomenon occurs in many species of Wood-sorrel, Poppy, Pheasant's Eye, Isopyrum, Crow-foot, Wood Anemone, Cinquefoil, Starwort, Chickweed, Saxifrage, Rock-rose, Anoda, Potato, Pimpernel, Jacob's Ladder, and Tulip (e.g. *Oxalis lasiandra*, *Papaver alpinum*, *Adonis vernalis*, *Isopyrum thalictroides*, *Ranunculus acris*, *Anemone nemorosa*, *Potentilla atrosanguinea*, *Stellaria graminea*, *Cerastium chloræfolium*, *Saxifraga Huetiana*, *Helianthemum alpestre*, *Anoda hastata*, *Solanum tuberosum*, *Anagallis phænicea*, *Polemonium cæruleum*, *Tulipa sylvestris*). In the Scabious given in the illustration opposite (*Scabiosa lucida*, figs. 225<sup>5</sup> and 225<sup>6</sup>), and in several Composites (*Bellis*, *Doronicum*, *Sonchus*, *Tussilago*, &c.) it is the peduncles bearing the capitula which bend; in many Umbelliferous plants (e.g. *Astrantia*



*alpina*, *A. carniolica*, &c.), it is the stalks of the umbels, and in some Cruciferous plants (e.g. *Draba aizoides*, *Arabis Turrita*, *Sisymbrium Thalianum*), the axes of the racemes. The above-mentioned Scabious and Composites exhibit a periodic inversion of the entire inflorescence in consequence of the inflection of the axis, and the radiating ligulate florets set round the margin of the capitulum serve to shelter the pollen of the central florets. Similarly in the Umbellifers named, the involucre of the separate umbels, being comparatively large, act in the same way. The fact is also worth notice that in some Willow-herbs (e.g. *Epilobium*



Fig. 225.—Protection of Pollen.

<sup>1</sup> Flowers of the Herb-Robert (*Geranium Robertianum*) in the daytime; the pedicels erect. <sup>2</sup> The same plant with its flowers pendent on curved pedicels, the position assumed during the night and in wet weather. <sup>3</sup> Bell-flower (*Campanula patula*) by day; the flower on erect pedicel. <sup>4</sup> Flower of the same plant inverted for the night or for wet weather, the pedicel being curved. <sup>5</sup> Capitulum of a Scabious (*Scabiosa lucida*) in the daytime; the peduncle erect. <sup>6</sup> Capitulum of the same plant at night or during rain, the peduncle curved and the capitulum inverted.

*hirsutum*, *E. montanum*, *E. roseum*), the flower-stalks themselves do not bend, but the long stalk-like inferior ovaries curve downward and straighten out again, periodically causing the flowers, which are of a flat salver shape, to alternate between a pendent and an erect position. The inflection of flower-stalks, or, of their substitutes, the ovaries, ceases as soon as the pollen of the flowers concerned has been removed by one means or another, and a shelter for it is no longer needful. The flower-stalks of *Saxifraga Huetiana* only continue to bend so long as the anthers in the flowers they support are covered with pollen, and the long ovaries of the Willow-herbs mentioned above only curve towards the earth on two successive evenings; the third evening,

when there is no longer any pollen to protect from rain and dew, they remain erect.

All these phenomena of inflection and straightening on the part of flowering axes and inferior ovaries are brought about in the same way as the periodic movements of petals and bracts by alterations in the tension of the tissues. These variations of tension are again due partly to vicissitudes in respect of heat and light, and of the degree of moisture of the air. But mechanical stimuli also play an important part, especially such shocks to the flower-bearing axis as are occasioned by the incidence of drops of rain and by gusts of wind. The fact that drops of water are found resting on the nodding or drooping flowers, if the latter are examined before sunrise when there is a heavy dew, or after a shower, tempts one to look upon the inflection merely as a consequence of the strain imposed upon the stalks by the increased weight of the water-laden flowers. No doubt this strain has something to do with the inflection, but it is equally certain that the drooping state does not disappear at once when the water has evaporated and the strain due to its weight has terminated. This persistence of the inflection at all events must be attributed to an alteration in the tension of the tissues of the stem, and no more than the first impulse can be derived from the weight of dew or the impact of drops of rain. Additional evidence of this is afforded by the facts that the process of bending is set up by rain falling on flowers and stem, even when it rolls off immediately, and that pedicels and peduncles also bend over whenever the entire plant is caused to sway about by the wind which precedes a downpour, the stems on these occasions always curving away from the direction of the wind, or, to use a nautical expression, to the lee side.

This phenomenon of the bending of stalks and drooping of flowers before the rain has actually begun looks almost as if the plant had the power of foreboding the approach of bad weather and of adapting itself beforehand in such a manner as to prevent any injury being subsequently inflicted upon it by that destructive agency. Such is the opinion of the peasantry in parts of Europe, and they look upon the inflections above described, as well as the closing of the heads of the Carline Thistle, which was mentioned further back, as a sign of imminent rain. There is, however, as already said, a mechanical explanation of the phenomenon dependent on a change in the tension of the tissues of the stem induced by the oscillations of the plant when subjected to the gusts of wind which usually precede rain, the change of tension being manifested externally by the persistence of the stem's inflection. Moreover, this lasting curvature of the stem may also be produced artificially by inducing the same kind of strain as is caused by the weight of the rain-drops or the vibration caused by rain and wind. If, for instance, you bend the pedicels of various species of *Oxalis* from the erect position they occupy in the middle of the day and hold them down for a time, or if you shake or knock them, the tissues forthwith undergo a change of tension which results in those stalks



becoming curved and the flowers drooping towards the ground instead of facing the sky as before. The same is true of the stalk of a Tulip (*Tulipa*), of the long peduncles of *Doronicum*, of the flower-bearing stems of *Asperula arvensis*, *Astrantia major*, *Cardamine pratensis*, *Lychnis flos-jovis*, and *Primula cortusoides*. If you try to straighten the stalks again afterwards you run a risk of breaking them. An interval of some hours elapses before this inflexibility disappears and the tensions existing before the act of mechanical stimulation are re-established and the stems become straight again.

These different changes in the direction and position of petals, bracts, flower-stalks and stems, which take place concomitantly with the alternations of night and day, of storm and calm, cloud and sunshine, often imply a complete transformation in the aspect of the vegetation within a very brief space of time. On warm summer days, when the sky is clear and the air still, the green of the meadows is sprinkled with the colours of innumerable open flowers. The stellate, salver-shaped, and cup-shaped flowers and inflorescences of Anemones, Ranunculuses, Potentillas, Gentians, and Composites are all wide open, so that the upper brightly-coloured surfaces of their flowers are visible from a great distance. Most of them are turned towards the sun, which enhances their brilliancy; several of the flowers and inflorescences—as, for instance, the Rock-rose (*Helianthemum*)—follow the sun, and face the south-east early in the morning, the south at noon, and the south-west in the afternoon. Countless flies, bees, and butterflies swarm and buzz round the flowers in the sunshine. When the sun sets a cool breeze springs up, and there is a copious deposit of dew on leaves and flowers. The insects withdraw to their homes to rest for the night, and the flowers seem to fall asleep too. Petals fold up, heads of flowers close, flowers and inflorescences bend towards the ground and exhibit the inconspicuous outer surfaces of their floral envelopes to the onlooker. Whilst the night lasts the meadow, drenched in dew, continues in a state of torpor, from which it is awakened once more by the warmth imparted by the sun when it rises next morning. A similar change of aspect occurs when a storm is brewing, when the meadow is swept by wind and rain falls upon the flowering plants. In this event also most flowers cover over or wrap up the parts liable to destruction in time to prevent material damage being done to their pollen.

Comparatively few among ordinary meadow plants appear to be in no way affected by these alterations in external conditions. Some seem to be able to dispense altogether with contrivances for protecting their pollen, for when once the flowers have opened the pollen-cases are left free and uncovered even on occasion of heavy showers. Thus, for example, in *Plantago* and *Globularia* the anthers are borne on long filaments and project in both good and bad weather out of the small flowers, which grow close together in spikes and capitula, and it would seem as though their pollen were exposed to inevitable destruction in case of wet. But closer inspection reveals that even these plants are not destitute of apparatus for the protection of the pollen. To the anthers themselves



is due the security enjoyed by the pollen developed from their tissues. For if dewy nights or wet weather occur after dehiscence has taken place and whilst the pollen is exposed at the apertures in the anther-cavities, the latter close up again and encase the pollen once more. The mature pollen is then protected from wet just as effectually as it was during the period of its maturation, for no injurious effect can be exercised by rain or dew through the walls of the anther upon the pollen-cells concealed within. When there is a return of warm, dry weather the anthers open afresh in the same manner as on the occasion of their first dehiscence. Precisely the same processes as were described on pp. 91-93 are repeated. If the anthers are unilocular with transverse dehiscence, like those of *Globularia* and the Lady's Mantle (*Alchemilla*; see figs. 226<sup>5, 6, 7, 8, 9, 10</sup>), the sutures open and shut like lips. If the dehiscence is opercular, as in the Bay Laurel (*Laurus nobilis*; see figs. 226<sup>11, 12, 13, 14</sup>), the valves shut down again and force the pollen adherent to them back into the open recesses of the anthers. Lastly, if the dehiscence is longitudinal and the anther-walls open outwards like folding doors and at the same time become revolute, as in *Thesium* and *Bulbocodium* (cf. figs. 226<sup>1, 2, 3, 4</sup>), the movement is reversed in wet weather, and the two valves close completely together again.

In the Arctic regions and amongst the mountains of Central Europe where copious deposits of moisture occur during the flowering season common to most plants, the number of species possessing anthers which open and shut periodically is not great. Besides those already named, i.e. *Bulbocodium*, *Thesium*, and the *Alchemilla*, only the Plantains (*Plantago*) and Ranunculaceæ, especially those with pendulous anthers (*Thalictrum*), remain to be mentioned as exhibiting this phenomenon particularly clearly. It appears to be much commoner in warmer parts, especially in sub-tropical and tropical regions; at all events, this periodic opening and closing of the anthers is exhibited to perfection in the following plants:—Cinnamon-trees, the Camphor-tree, the Laurel and Lauraceous plants generally, Araliaceæ and Cycadææ, the various species of *Ricinus* and *Euphorbia*, *Cistus*, the Vine (*Vitis*), and indeed the majority of Ampelideæ, the Tulip-tree and Magnolias (*Liriodendron*, *Magnolia*), and lastly, amongst Conifers the genus *Cephalotaxus*.

The phenomenon in question is the result of changes in the condition of the air in respect of moisture, and depends upon the contraction and expansion of the hygroscopic cells which we noticed in the last chapter as being developed underneath the epidermis of the anther-walls. As in the case of the movements of the involucre bracts on the capitula of the Carline Thistle, the process is only affected by heat inasmuch as the relative degree of moisture in the air alters with a rise or fall of temperature. Seeing that under ordinary conditions variations of temperature and increase or decrease of humidity are connected with the alternation of day and night, it is clear that a periodicity will also be manifest in the opening and closing of anthers, and that in the evening when the degree

of moisture is increased the anthers will close, remain shut throughout the night, and not begin to open again till after sunrise, when the degree of moisture is diminishing.

In cases where both the anthers and the petals of a flower open and close periodically, the corresponding movements are for the most part accomplished simultaneously; but if the cause of the movement is different for petals and anthers it may happen that there is no such unison. For instance, after prolonged rain, the petals of *Bulbocodium* may open under the influence of a

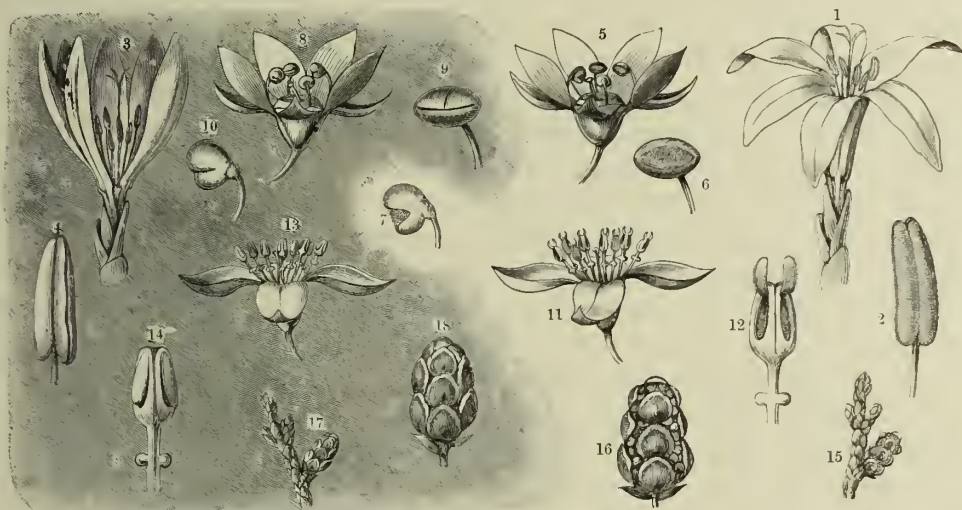


Fig. 226.—Protection of Pollen.

- <sup>1</sup> Flower of the *Bulbocodium* with the perianth and the anthers open as they are when the sun is shining and the air dry. <sup>2</sup> An anther from the same. <sup>3</sup> Flower of *Bulbocodium* in moist air; the perianth half open, the anthers closed. <sup>4</sup> An anther from the same. <sup>5</sup> Flower of the Lady's Mantle (*Alchemilla*) with its anthers open in a dry atmosphere. <sup>6</sup>, <sup>7</sup> Anthers from the same. <sup>8</sup> Flower of the Lady's Mantle with its anthers closed in rainy weather. <sup>9</sup>, <sup>10</sup> Anthers from the same. <sup>11</sup> Flower of the Bay Laurel (*Laurus*) with its anthers open in a dry atmosphere. <sup>12</sup> An anther from the same. <sup>13</sup> Flower of the Bay Laurel with its anthers closed in wet weather. <sup>14</sup> An anther from the same. <sup>15</sup> Stamiferous flowers of *Juniperus Virginiana* in a dry atmosphere. <sup>16</sup> The same magnified. <sup>17</sup> Stamiferous flowers of *Juniperus Virginiana* in wet weather. <sup>18</sup> The same magnified. <sup>1</sup>, <sup>3</sup>, <sup>15</sup>, <sup>17</sup> natural size. The rest  $\times 2$  to 8 times.

warm spell of sunshine, whilst the anthers still remain closed owing to the excessive moisture of the atmosphere.

Anthers close up much more quickly than petals on the approach of danger. They usually take only a few minutes, and in many cases not more than half a minute. The anthers of the Bastard Toad-flax (*Thesium alpinum*) shut up within thirty seconds of their being moistened. In this plant the process of closing is rendered additionally interesting by the fact that the moistening of the anther-walls is effected by peculiar tufts of hairs projecting from the perianth. The briefest possible description of this phenomenon will be given here. The open flower of *Thesium* has the limb of its perianth turned to the sky. This position is maintained unchanged day and night, and even the occurrence of bad weather does not cause any alteration in the direction of the flower-stalks or the position of the flowers. Hence rain-drops falling from above and the dew formed on

clear nights must inevitably rest on the open flowers. The immediate wetting of the entire flower is, however, prevented by peculiarities in the form of the limb. The anthers close with great celerity upon the deposition of the drops, the explanation being that the perianth-lobes are connected with the anthers standing in front of them by a bunch of twisted hairs which not only are themselves peculiarly susceptible of being wetted, but conduct the water to the anthers and so cause the anther-walls to close.

A characteristic manner of protecting the pollen by means of the anther-walls after the pollen has been set free, and when it is ready to be carried away by insects, may be observed in several Composites (e.g. *Onopordon*, *Centaurea*). There is no material difference between these plants and the other Composites discussed on p. 114 in respect of the structure of the tube of syngenesious anthers, the discharge of the pollen into that tube, or the structure of the style and its situation inside the anther-tube; but an essential distinction exists in the fact that the pollen is conveyed to the mouth of the tube not through the elongation of the style but the contraction of the filiform supports of the anther-cylinder. These filaments in *Onopordon* and *Centaurea* contract in response to mechanical stimuli, and in shortening they pull down the anther-tube with them. The top of the style thereupon becomes visible, for the style is sheathed in the tube, and does not shorten when the filaments do so nor change its position. The pollen resting on the style is consequently exposed, and appears in the form of a pulverulent mass on the top of the style surmounting the anthers. If the mechanical stimulation of the filaments is due to the hovering of an insect about the capitulum, the pollen is no sooner exposed than it is brushed off by the insect, and the entire contrivance is obviously so devised that the same insects as cause (by the touch of their legs or probosces) the contraction of the filaments, the retraction of the anther-tube, and the exposure of the pollen may be themselves loaded with the pollen. Up to the moment of the insect's visit, however, the pollen is hidden in the sheath formed by the anthers, and this position is of advantage to it inasmuch as it is there sheltered from rain and dew. The Composites in question have their capitula erect. The capitula of *Onopordon* include neither movable ligulate ray-florets nor radiating bracts capable of closing. *Centaurea* has trumpet-shaped marginal florets, but they do not possess the power of arching over and protecting the tubular florets of the centre. The stalks of the capitula become neither pendent nor nodding in wet weather. In short, the pollen of these particular Composites is destitute of any of the various means of protection which are present in other genera of the same family and which have just been discussed. But instead, the anther-tube itself undertakes the task of sheltering the pollen after the latter is liberated until the moment when the insects which are to carry it away alight upon the flowers.

We need only notice incidentally that extrorse anthers, which turn their recesses filled with coherent masses of pollen towards the earth and their backs to the sky are also to a certain extent protected against wet. A more impor-



tant provision at all events consists in the fact that the injurious effect of rain or dew on the pollen-cells may be obviated by certain special sculpturings on the surfaces of these cells. Reference has already been made to such cases at the conclusion of the last chapter. They are on the whole rare, and are limited apparently to plants of the tropical and sub-tropical regions. The pollen of the beautiful climbing *Cobaea scandens* (cf. fig. 217<sup>1</sup>), one of the Polemoniaceæ, will serve as an example. On the surface of this pollen may be observed a number of little pits with angular rims which make it look at first sight almost like a honey-comb. The pits are not, it is true, so deep as those of a honey-comb, but they are deep enough to prevent the air with which they are filled from being displaced by water dropping upon the pollen. Thus air remains in the pits and thereby affords protection from wet, for it forms an intermediate layer separating the thin parts of the cell-membrane from the water. The thick layers of the cell-membrane which project in ridges are still liable to be wetted, but water cannot penetrate at once through them into the interior of the cell, and such an entrance it is that constitutes the greatest danger to the pollen. A gradual absorption of watery liquid—especially that which is derived from the cells of the stigma—is not only not avoided, but is even necessary for the subsequent development of the pollen-cells.

The instances chosen hitherto for the exemplification of the numerous contrivances whereby the pollen in flowers is protected against wet belong, for the most part, to the category of those which have developed one form of protective apparatus only. Frequently, however, two or even three methods of defence co-exist, so that in case one contrivance should fail there is another in reserve. This occurs in cases where the plant has only a meagre stock of pollen, where the number of flowers on one individual and the quantity of pollen-cells produced from each flower are small, and therefore there is not much pollen to waste, where the time allotted to a plant in which to unfold all its flowers is extremely limited, and where the transport of the pollen from flower to flower is accomplished exclusively by flying insects, whose visits are sometimes delayed for several days when the weather is unfavourable. To mention a few instances with more than one means of protection, in many *Anemones* and *Crow-foots*, the *Hepatica*, the *Rock-rose*, and the *Wood-sorrel* (*Anemone*, *Ranunculus*, *Hepatica*, *Helianthemum*, *Oxalis*), not only do the petals close over the pollen-laden anthers, but the flower-stalks also bend, causing the flowers to nod. In the *Daisy* (*Bellis*), the *Corn Sow-thistle* (*Sonchus arvensis*) and many other *Composites* not only do the ligulate florets of the ray incline towards one another and form a roof over the pollen of the central florets in cloudy weather and in the evening, but in addition the peduncles become bent or pendent. In *Podophyllum peltatum* the pollen is sheltered by the bell-shaped flower, but in addition to this the peltate foliage-leaves are also spread out over the flowers and act as umbrellas. The synchronous closing of both anthers and petals over the pollen when rain threatens is a phenomenon that may be easily observed in a number of plants, as, for instance, in *Bulbocodium* (cf. figs. 226<sup>1, 2, 3, 4</sup>).

The fact is also worthy of note that identical means of protection have not always been evolved by members of the same family of plants. One has one method of defence, another another. This diversity is exhibited particularly by the various genera of Solanaceæ, and by the multifarious species of the genus *Campanula*. In the Solanaceæ we find the following variety of contrivances according to the genus. The flowers of the Potato (*Solanum tuberosum*) fold up in the afternoon and assume an inverted position owing to the curvature of their stalks for the night, but only maintain it whilst the night lasts. The next morning the flower-stalks straighten, and the flowers unfold again. The Deadly Night-shade (*Atropa Belladonna*) has its flowers inverted during the whole of the flowering season, and it is therefore not necessary for the corollas to open and shut. The flowers of the Mandrake (*Mandragora vernalis*) remain erect, but in the night and in rainy weather the tips of the upright corolla-lobes close over the pollen-covered anthers inside. As regards the different Bell-flowers (*Campanula*), those which have very long peduncles—e.g. *Campanula carpathica* and *Campanula patula* (cf. figs. 225<sup>3</sup> and 225<sup>4</sup>)—are only pendent in the night and in bad weather; by day and in fine weather they are erect. They exhibit pronounced periodic movements resulting in the curvature of their axes. In other Bell-flowers with shorter stalks—e.g. *Campanula persicifolia*, *C. pusilla*, *C. rotundifolia*—the buds nod before they open and continue in this position throughout the time of flowering, whilst in those species wherein the flowers are crowded together in heads and have very short stalks—e.g. *Campanula Cervicaria*, *C. glomerata*, *C. spicata*—there is in general no curvature of the axes, but the flowers remain upright and guard themselves against rain by means of an inflection of the points of the corolla towards one another which closes the mouth of the bell. Lastly, in the Venus' Looking-Glass, a plant nearly related to the Bell-flowers, the flower closes by means of deep folds formed in the corolla.

When contrivances have to be described which subserve several purposes at the same time, it would lead to confusion to attempt to say everything that there is to be said about them in one place. In such cases it is much more to the purpose to keep one object alone in view even at the risk of appearing one-sided to a hasty reader. This remark is particularly applicable to the means of protection just described as being adopted by plants to preserve their pollen from wet; for there is no question but that most of these contrivances are capable of rendering other services to the plants in question besides the one specified. In many cases the closing of petals effects not only the protection of the pollen, but also its transference to neighbouring stigmas in the event of a dearth of insect-visitors, as will be explained in a subsequent chapter. If a flower-cup filled at the bottom with honey remained open to the rain the honey would be immediately spoilt and would no longer act as an allurement to insects. Hence we may infer that the shutting of the entrance to the interior of the flower, the construction of the corolla-tube, and the change to a nodding position in the case of melliferous flowers preserve not only the

pollen, but also the honey from being spoilt by the wet. The narrowing of the corolla-tube and the barricading or complete closing of the entrance to the flower also serve, on the other hand, to keep out certain honey-seeking creatures whose visits would not be advantageous to the plant. Finally, these same contrivances may ward off also such insects as would remove the pollen without conveying the least particle of it to other flowers. In connection with this last function there exist, no doubt, special adaptations besides, one of the most striking of which occurs in the Monkey Flower (*Mimulus*) and in the Hemp-Nettle (*Galeopsis*), and is shown in the illustration of a stamen of *Galeopsis angustifolia* (fig. 216<sup>19</sup>, p. 91). In this instance the anthers are furnished with two lids which can only be opened by a certain proportion of the insects visiting the flowers. Insects with bodies of such a size that when they enter the flower they rub the pollen from the anthers on to their backs are able to lift the lids of the anthers by brushing against them, and they thus expose the pollen. On the other hand, smaller animals which would not load their backs with pollen on visiting the flowers in question or would not convey it to the stigmas of other flowers are not strong enough to open the anthers. Thus the pollen is effectively protected by means of these lids against the detrimental action of small-sized plunderers.

#### DISPERSION OF POLLEN BY THE WIND.

At the beginning of the last chapter it was stated that the medium wherein the transport of the pollen to the stigmas takes place is, in the great majority of Phanerogams, the air. For the conveyance of pollen between flowers situated at a distance from one another there exist two main agents, viz. the wind and insects. Hence Phanerogams have been distinguished by botanists into "anemophilous" or wind-fertilized, and "entomophilous" or insect-fertilized plants. But these terms, which are adopted in most works on Botany, can only be used in a strictly limited sense. It is no doubt true that there are plants in which the transference of the pollen to the stigmas is effected exclusively by the wind, and others in which the equivalent process takes place solely through the intervention of animals; but, on the other hand, it has been ascertained in the case of a large number of plants that whereas shortly after the flowers open small creatures carry off the pollen and convey it to other flowers, later on, when the flowering period is drawing to a close, the pollen is committed to the wind and by it transferred to the stigmas of neighbouring blossoms. The best instances of this are afforded by several of the Rhinanthaceæ, as, for example, *Bartsia* and the Toothwort (*Lathræa*), and by many Ericaceæ, such as *Calluna vulgaris* and *Erica carnea*, but many more could be mentioned. The conformation of the various parts of these flowers when they first open renders a dispersal of the pollen by the wind impossible; but in fine weather insects visit them in large numbers, and in the act of sucking the honey load themselves with pollen



which they afterwards convey to the stigmas of other flowers. Subsequently, however, the conditions are reversed, the supply of honey is exhausted and insects stay away; but, on the other hand, the filaments bearing the anthers have elongated, the pollen-sacs are consequently exerted above the mouth of the corolla, the pollen contained in them is laid bare, and, at the proper time, is blown away by the wind to the stigmas of younger blossoms. Plants of the kind thus appear to have a second contrivance in readiness in case the first fails, so that in any circumstances the object of flowering may be attained. This is indeed a matter of urgent necessity. How easily may it happen that insects are kept away for a long time by unfavourable weather or that they pay but a few visits. Most plants, therefore, take the precaution to provide that under such circumstances the expenditure of energy involved in the production of flowers shall not have been in vain.

It would be inconsistent with the plan of this book to discuss here all the remarkable adaptations which have been evolved for the purpose of providing a supplementary means of dusting the stigmas with pollen in the event of an absence of insects, but it is necessary to make preliminary mention of this one arrangement whereby many flowers, originally entomophilous, subsequently become anemophilous, because it enables us to determine the proper degree of significance to be attached to the division of plants into anemophilous and entomophilous species.

As would naturally be expected, it is, speaking generally, only pollen which is of dusty or floury consistency that is transported by the wind. If it is true, as gardeners assert, that the pollen of Azaleas, which oozes from the anthers in the form of sticky fringes, has on occasion been torn away and conveyed to the stigmas of neighbouring flowers by the wind, the occurrence can only be looked upon as accidental. In ninety-nine cases out of a hundred the viscid strings, if detached by the wind, would not be conveyed to the stigma of another flower, but would adhere to the outside of the calyx and petals, or to the leaves and stem, and would there perish. The same remark applies also to pollen-cells which are bound together into little lumps by oil and viscid substances, or by acicular processes on the outer layer of the cell-membranes. Only in the rarest instances are they carried by the wind to the stigmas of flowers in the vicinity. These are primarily adapted to becoming attached to the bodies of winged insects.

All the more remarkable, therefore, is the fact that in certain water-plants the pollen, though cohering in sticky masses, is blown by the wind on a kind of little boat to the stigmas which are raised above the surface of the water. The phenomenon was first observed in the case of *Vallisneria spiralis*, an aquatic plant which grows in still water, and is widely distributed in Southern Europe. It is, for example, very luxuriant in the ponds, canals, and shallow inlets along the shores of the Lake of Garda, and we will select it as an illustration in the account which follows. The reader is requested first of all to look at the figure on p. 667 of vol. i. It represents a plant living under water with strap-

shaped leaves arranged in fascicles at the ends of the creeping stems which are attached to the mud by root-fibres. In the axils of these leaves a variety of buds are produced—in some cases one only which constitutes the starting-point of a new creeping shoot; in others three close together, one of which grows in length parallel to the bottom and develops a foliage-bud at its extremity, whilst the two others grow straight upward, or there may be two, of which one elongates in a horizontal direction, whilst the axis of the other rises towards the surface of the water. Each of the upward-growing shoots terminates in a kind of bladder composed of two concave and somewhat transparent bracts, one of the pair overlapping the other so as to close the bladder securely. Within these bladders are the flowers. Of the individual plants some develop female flowers only, others male flowers only. The former occur singly in the bladders. Each possesses a long cylindrical inferior ovary crowned by three relatively large stigmas with bi-lobed apices and fringed margins. The stigmas are surrounded by an envelope consisting of an upper whorl of three small abortive petals and a lower whorl of three large ovate-lanceolate sepals. These floral segments are invariably so disposed as to allow the finely-fringed margins of the stigmas to project somewhat beyond the perianth-lobes so that pollen may be caught by the fringes from the side. This is also the reason why the three inner perianth-lobes are stunted, for if they were as large as the outer three the stigma would be covered in at the side and no adhesion of pollen could take place. When the stigmas have reached the stage of being adapted to the reception of pollen, the top of the bladder investing the flower splits; the ovary elongates, flower and stigma are pushed up above the envelope, and appear on the surface of the water, where they are spread out in the medium of the air (see fig. 227). The phenomenon described is only rendered possible by the fact that the stalk of the pistilliferous flower lengthens to an extraordinary extent, and does not cease growing until the flower it bears has reached the surface of the water (*cf.* vol. i. p. 667).

The case of the staminal flowers is utterly different. They are not solitary, but grow in large numbers in a bunch on an axis which stands up in the middle of the investing bladder. The two leaves composing the bladder become disjoined under water, and expose the raceme of spherical buds. The buds are still *in situ* on the rachis, which remains quite short, the inflorescence being held at a height of about 5 centimetres above the mud, as is shown in fig. 155, p. 667, vol. i.

Shortly afterwards one of the most wonderful processes exhibited by the vegetable world is gradually accomplished. The flower-buds hitherto connected with the axis of the raceme by diminutive stalks become detached, ascend in the water, and float about on the surface. At first they are still closed and globular, but soon afterwards they open. The three concave leaflets (sepals) forming the outer whorl of the perianth, which have up to that time been arched like cowls over the stamens, are thrown back and assume the appearance of three boats connected together at one spot, and the stamens, which were originally three in number, but of which only a pair are now furnished with anthers whilst the third

has remained rudimentary, project obliquely up into the air (see fig. 227). The opening of the petals is immediately followed by the dehiscence of the anthers. The coat of the anther shrivels up rapidly, leaving nothing but a little flap upon which the pollen-cells rest. There are generally only 36 pollen-cells contained in each anther. These are comparatively large and very sticky, they cohere together and form a mass of pollen which is borne upon the thick stamen. Notwithstanding the fact that they are very near the surface of the water, the masses of pollen-cells are not easily wetted. The three sepals underneath them form, as has been said, three boats which respond to the slightest movements of the water without upsetting, and therefore protect their freight from wet to

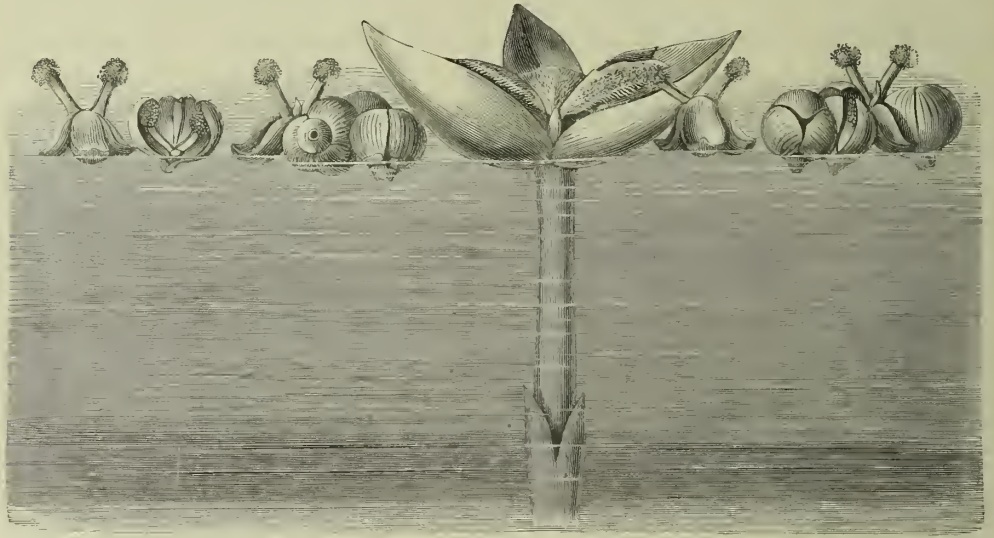


Fig. 227.

Flowers of *Vallisneria spiralis* floating on the surface of water. In the middle a female flower with several male flowers on either side of it in various stages of development; some still closed, some in process of opening, some open with their boat-shaped perianth-lobes thrown back. Projecting from the open flowers are the stamens. An open anther is attaching its pollen to the fringed stigmatic margin of the female flower.  $\times 10$ .

perfection. These little floats are blown hither and thither by the wind and accumulate in the neighbourhood of fixed bodies, especially in their recesses, where they rest like ships in harbour. When the little craft happen to get stranded in the recesses of a female *Vallisneria* flower they adhere to the tri-lobed stigma, and some of the pollen-cells are sure to be left sticking to the fringes on the margins of the stigmatic surfaces.

Directly after the adhesion of the pollen, which takes place in the manner shown in fig. 227, the female flower is drawn down under the water. The long flower-stalk assumes a spiral form, and its coils close up so tightly together that the ovary, or young fruit as it now is, is brought to rest at quite a small distance above the muddy bottom of the water.

Up to the present time the conveyance by the wind of adhesive pollen on floats composed of the perianth of the flower is known to exist in the widely-



distributed *Vallisneria spiralis*, in *Vallisneria alternifolia*, which is indigenous in tropical Asia, in *Enalus acoroides*, which grows in the Pacific and Indian Oceans, in *Hydrilla verticillata*, *Elodea Canadensis*, and a few species of the genus *Lagarosiphon*, native at the Cape and in tropical Africa—only 13 species all together, comprised in the little family of Hydrocharidaceæ. This number is almost inappreciable compared with that of the species which produce pollen in the form of fine dust or loose flour, and wherein the pollen is dispersed exclusively and throughout the period of flowering by the wind which blows it away in clouds. It would not be far out to put the number of wind-pollinated plants at 10,000, *i.e.* at about a tenth of the total number of Phanerogams. To this category belong the Conifers, Oaks, Beeches, Hazels, Birches, Alders, Poplars, Walnut-trees, Mulberry-trees, Planes, and the majority of Palms. All these are of the nature of lofty trees, and usually grow in numbers together, each being associated with others of its own kind so as to form extensive woods or plantations, characterized by a close association of individuals. To these must be added the Grasses produced in meadows, prairies, and savannahs; the Sedges, Reeds, and Rushes characteristic of marshes; the Cereals of our fields; Hemp, Hops, Nettles, and Plantains; the common Pondweeds growing in still or running water, and many other plants belonging to families of the most widely different kinds.

One striking characteristic of these exclusively wind-fertilized plants is the absence of fragrant and bright-coloured flowers. The floral-leaves are comparatively small, of a greenish or yellowish colour, and stand out very little, if at all, from the foliage. The interior of the flower is destitute of honey and perfume. It is of no advantage to these flowers to be visited by insects, and accordingly they have no need of any of the means of alluring bees, butterflies, or flies. Hence the absence of odorous substances, of sweet juices, and of brightly-coloured corollas contrasting with the green foliage and visible from afar. We do not mean to say, however, that the flowers of the plants in question are altogether shunned by insects. Many insects covet the pollen itself, and not infrequently they may be seen hovering about the catkins of Hazels and Birches, on the spikes of Plantains, the panicles of Grasses, Rushes, and Reeds, collecting or devouring the pollen. But these visitors play but a very subordinate part in the dispersion of the pollen. By knocking against parts of a flower that are covered with pollen-dust they may, of course, cause some to fall out, but in so doing they only render a service to the plant if the right wind happens to be blowing at the moment and conveys the pollen to the stigmas. If there is no wind, or it blows in a wrong direction, the plants are more likely to be injured than aided by the insects' visits; for, as the stigmas are not brushed by the pollen-seeking insects and therefore receive no deposit of pollen from them, and, on the other hand, the pollen that they shake out is not likely to be carried to the corresponding stigmas if the air is still, it usually happens that anemophilous plants of the kind thus suffer a loss of pollen without obtaining any compensating advantage.

As has been above implied, however, it is not every aërial current that is adapted to serve as an agent for transferring pollen to stigmas. The least favourable winds are those which are combined with atmospheric deposits. Besides the fact that the pollen-dust would be washed away from its resting-places by the rain and carried to the ground, it must perish in consequence of the soaking. Storms of wind without rain are also anything but beneficial, for they forcibly whirl away any pollen that they encounter and carry it in one direction only, and, as but a small proportion, if any, of the stigmas requiring to be fertilized lie in the path of the wind, the greater part of the pollen is wasted.

The result aimed at is best achieved when the pollen-dust, after being removed from the spot where it has been produced or deposited, is distributed uniformly over an ever-extending area, becoming, in a manner of speaking, diluted and forming a cloud of gradually increasing dimensions but diminishing density, so that the thousands of loose pollen-cells which have up to that time been crowded together within the province of the flower and contained in a space about the size of a pin's head are scattered over an area many million times as great. A gradual dispersion of the kind is only occasioned by a gentle wind. The light breezes which sweep through valleys shortly after sunrise, ascending air-currents such as one perceives quivering over heated plains at noon, the alternating land and sea breezes of the coast-winds which, in passing over cornfields, set the corn in gentle waving motion, and in woods cause a scarcely audible rustle—such are the most propitious agents of pollination. It is easy to observe how, at the proper season, under the influence of a gentle wind of the kind one little cloud of dust after another detaches itself from the flowers of the plants in question and slowly soars away. Owing to the fact that the motion of aërial currents is undulatory and undergoes at short intervals alternate augmentation and diminution, the first motion of the pollen as it dissipates itself is also in waves; but the little cloud is soon withdrawn from observation as it proceeds on its way, and the only thing we can clearly discern is that pollen, like dust raised on a road, ascends in an oblique direction.

The form and distribution of the stigmas to be covered with dust-pollen are also in harmony with these conditions. Most plants, whose pollen is in the form of dust, and transported entirely by currents of air, have diœcious or monœcious flowers, and those which develop hermaphrodite flowers exhibit complete dichogamy, that is to say, the andrœcium and gynœcium ripen at different times, so that when mature pollen is being discharged from the anthers of a flower the stigmas of the same flower are already withered, and therefore no longer in a condition to receive the pollen-cells, or else they are still so immature that they cannot be covered with pollen. Any possibility of the transference of pollen from the anthers to the stigmas situated close to them in the same flower being attended with success is as effectually excluded in dichogamous plants as it is in monœcious and diœcious species, and the pollen has to be blown to other flowers in the neighbourhood whose stigmas happen to be in

the receptive stage of development. In all these dichogamous plants the flowers with stigmas in the receptive condition are situated higher than the anthers from which mature pollen is being committed to the wind. If you look at any of the species of Plantain (*Plantago*) a few days after they have begun to flower, you find that only the styles with their stigmas ready to receive the pollen project from the uppermost flowers in each spike, whilst the flowers from which pollen is being shaken by the wind occupy the lower parts of the spike.



Fig. 228.—The common Alder (*Alnus glutinosa*).

Branch with flowers that open before the leaves are unfolded; the male flowers grouped in the form of pendent catkins, and above them the female flowers grouped in the form of little spikes. <sup>2</sup> Leafy branch at the top of which are the rudimentary inflorescences for the following spring.

In these lower flowers the stigmas are already withered, in the upper ones the anthers are still closed. Therefore, in order to reach the receptive stigmas, the pollen must travel upwards. The same conditions are found in most species of Sorrel (*Rumex*), in the Wall-Pellitory (*Parietaria*), in Saltwort (*Salsola*), in Arrow-grass (*Triglochin*), and in Pondweeds (*Potamogeton*), and many other plants with hermaphrodite but perfectly dichogamous flowers (*cf.* figs. 236 and 237).

This phenomenon is still more strikingly exhibited by monœcious plants, *i.e.* where male and female flowers occur on the same individual. In the Oak, the Beech, the Alder, &c., the catkins of mature polliniferous flowers hang down



from the branches in the form of swinging tassels whilst the flowers containing mature stigmas are always above them, whether situated on the same or on adjoining branches (*cf.* fig. 228). In Fir-trees, only the pendent lateral branches of the boughs bear the male inflorescences, which at a distance look almost like red mountain-strawberries, whilst the female inflorescences stand up in the form of little cones on the top of the same boughs like tapers on a Christmas-tree; indeed, many Fir-trees bear the female flowers only on the highest branches close to the summit, and on the lower boughs none but male flowers, and under such circumstances pollen could not possibly reach the stigmas if it were only carried by the wind in a horizontal direction. Even in dioecious plants (*i.e.* where the male and female flowers are on distinct individuals) this relatively inferior situation of the staminal flowers is often to be observed, the end being attained by the fact that the individuals bearing male flowers grow less high than those bearing female flowers. Thus, for example, in Hemp-fields one may see that the plants discharging pollen never reach the same height as those whose flowers are to receive the pollen. Exceptions to the rule do, it is true, appear to exist in the Bulrush (*Typha*), the Bur-reed (*Sparganium*), and many species of Sedge (*Carex*), which possess monœcious flowers, inasmuch as in them the male flowers are situated above the female; but in consequence of the non-simultaneous elongation of the axis, it usually comes about that the mature female flowers of a plant whose stem is amongst the older and taller ones rests at a higher level than the male flowers of the individual next to it whose stem is younger and shorter, and it is easy to convince one's self by observation that here also the pollen is not conveyed by the wind in a horizontal direction but obliquely upwards, and is wafted to the stigmas of neighbouring plants.

This must not, of course, be looked upon as implying that when pollen is dispersed by the wind none descends; but it is unquestionably true in the majority of cases that the clouds of pollen which are carried off by moderate winds at first soar upwards and either reach the stigmas awaiting them at a higher level direct in their way, or else, later on, when the air is still and the pollen-cells are scattered over a wider space, they sink slowly down, leaving a deposit on the stigmas, just as when dust is raised in a room it ends by slowly falling again and covering the furniture with a uniform layer.

In some species at the very moment when the anthers burst open the pollen is ejected violently into the air and ascends obliquely in the form of a little cloud of dust. In this country a good example of this phenomenon is afforded by the Nettles. Anyone standing in front of a bed of Stinging Nettles on a bright summer morning, and waiting until the first rays of sunshine fall on the flowers, will be surprised to see small pale-coloured clouds of dust ascending here and there from amidst the dark foliage. At first the clouds are solitary, and are given off at measurable intervals; by degrees they become more frequent, and at times one may see five or six or more arising at the same moment and at no great distance from one another. But gradually the little explosions become less frequent again, and

in another half-hour there is an entire cessation of the phenomenon. On inspection one easily discovers that it depends on the fact that the filaments bearing the anthers are coiled in the bud, and suddenly spring up at the same moment that the dehiscence of the anthers takes place.

The species of the genus *Parietaria* and many tropical *Urticaceæ* behave in the same manner in this respect as our Nettles. As an instance may be taken *Pilea microphylla* (also known under the name of *Pilea muscosa*), which grows



Fig. 229.—The Paper Mulberry-tree (*Broussonetia papyrifera*).

<sup>1</sup> Leafy branch with capitulum of female flowers. <sup>2</sup> Piece of a branch stripped of its foliage with spike of male flowers. <sup>3</sup> An unopened male flower in longitudinal section. <sup>4</sup> An open male flower in longitudinal section; two of the filaments are still tucked in, one has sprung up and is expelling the pollen from the opened anthers. <sup>5</sup> An open male flower with all its stamens already uncoiled and the pollen discharged from the anthers. <sup>6</sup> Two female flowers with long hairy stigmas. <sup>1</sup>, <sup>2</sup> natural size; <sup>3</sup>-<sup>6</sup>  $\times 4$ - $5$ .

native in Central America, and is often raised in botanic gardens with a view to demonstrating the phenomenon here alluded to. One only has to sprinkle the plant with water at a time when it is covered with flower-buds and then take it out of the shade into the sunshine, and the phenomenon is immediately exhibited. All over the plant the flower-buds explode, and a whitish kind of pollen is discharged into the air in the form of a little cloud. Many *Moreæ* also display this phenomenon, as, for example, the Paper Mulberry-tree (*Broussonetia papyrifera*), an illustration of whose flowers is given in fig. 229. The male flowers are arranged in spikes (229<sup>2</sup>), and each flower consists of a sepaloid perianth with four stamens

upon it. The filaments are very thick and, in the closed bud, are tucked in (229<sup>3</sup>); they are in a state of tension like a spring, but as soon as the cup-shaped perianth opens the filaments spring up one after another, whilst at the same instant the anther-cavities burst open and the pollen is ejected with force into the air (229<sup>4</sup>). When all the anthers are empty the filaments curve backwards (229<sup>5</sup>), and soon afterwards the entire spike of flowers drops off the axis, it being no longer of any value to the plant.

In all these plants ejection of the pollen only ensues when a light, dry wind



Fig. 230.—The Ash (*Fraxinus excelsior*).

<sup>1</sup> Small bifurcating branch, the left-hand limb of the fork bearing male flowers, the right-hand limb bearing hermaphrodite flowers. <sup>2</sup> Hermaphrodite flower. <sup>3</sup> Two anthers; the upper one open, the lower one still closed. <sup>1</sup> natural size; <sup>2</sup>, <sup>3</sup>  $\times 5$ .

blows at sunrise and causes an alteration in the tension of the tissues concerned. If there is no wind at all, or the air is close and damp, or if it rains, the opening of the flowers and ejection of the pollen do not take place, or rather they are postponed until the atmosphere has become dry again and a breeze arises which causes the flowering branches to sway about. The results of actual observation are of importance to a proper understanding of the dispersal of pollen-dust. For it thus appears that the air in motion has to start two processes which supplement one another, and must operate in rapid succession if the pollen-dust is to reach the right place and not be lost. The same current of air which causes a liberation and expulsion of the pollen by shaking the flowering axes and by altering the tension of the tissues of the flowers, also carries the pollen away from the spot where it has been produced

and conveys it to its destined goal; and this statement applies to the full extent not only to the case of resilient stamens, but also to all other instances of anemophilous pollination where the pollen is in the form of dust.

A similar phenomenon is observed in the case of plants with short, thick filaments and comparatively large anthers filled with pollen of a floury consistency. The *Phillyrea*, the Pistachio-nut (*Pistacia*), the Box-tree (*Buxus*), and most Ashes, especially the common Ash (*Fraxinus excelsior*, see fig. 230), may serve to illustrate this group of plants. The development of the carpels in each flower precedes that of the pollen. At a time when the relatively large fleshy stigmas stretch out far beyond the limits of the inconspicuous floral envelope, and are already capable of taking up the pollen, the anthers may be



seen to be still tightly closed (230<sup>1</sup> and 230<sup>2</sup>). The latter do not open till two or three—often even as much as four—days later, and only then in the event of the air being dry. Dehiscence is accomplished by longitudinal fissuring of the anther-lobes. The edges of these fissures contract very speedily, so that each of the pair of anther-lobes is converted into an open recess wherein the pollen lies in the form of a floury or powdery mass (230<sup>3</sup>). Just before dehiscence the

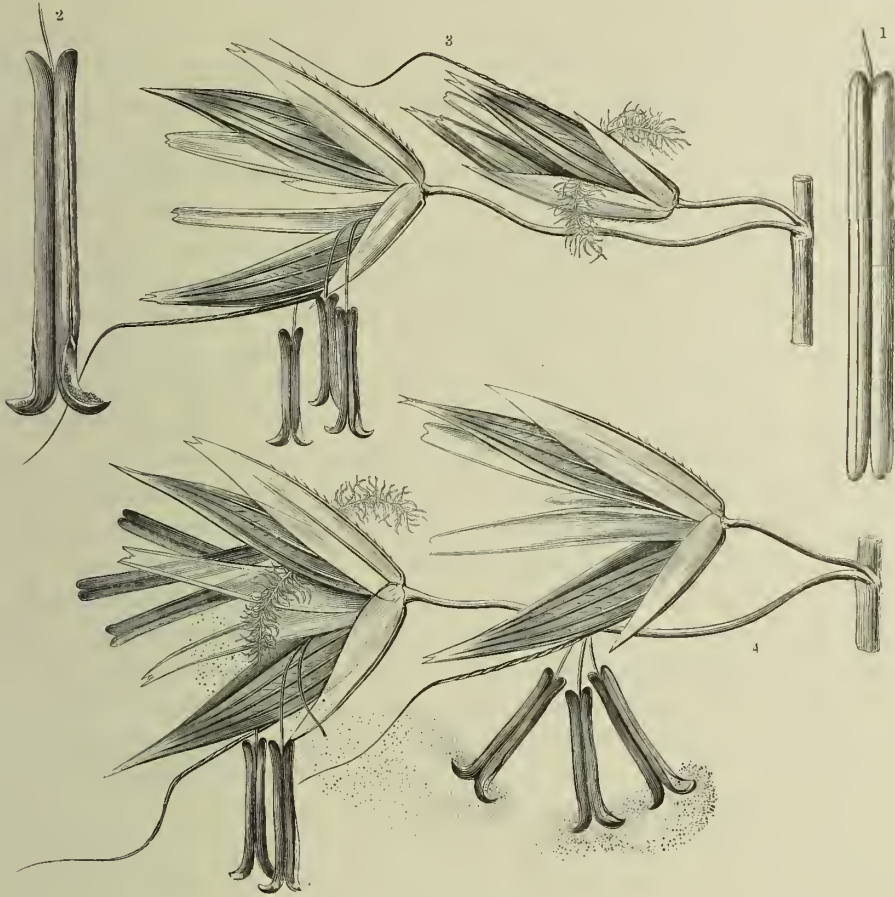


Fig. 231.—*Avena elatior*.

<sup>1</sup> A closed anther. <sup>2</sup> An open anther. <sup>3</sup> Spikelets on a calm day with glumes distended and anthers pendulous. <sup>4</sup> Spikelets in a wind. The pollen escaping from the pendulous anthers in the spikelets to the right; in that to the left (and below) the anthers (two only remaining) have shed their pollen; in a third flower (in the same spikelet as the last-mentioned) the anthers are still closed and in process of being exerted. 1, 2  $\times 12$ ; 3, 4  $\times 5$ .

anthers place themselves in such a position as to ensure the fissure being turned upwards, so that the recesses full of pollen are not emptied so long as the air is still. It is only when the flowering branches begin to sway to and fro that the pollen falls out of the loculi and is blown away in the form of a cloud of dust by the same breeze as set the boughs in motion.

In another group of plants the anthers are borne on long filaments, and are set oscillating and vibrating by the least breath of wind, the pollen being in

consequence discharged in little pinches as though from a sugar-sifter. If the flowers of this kind of plant contain pistils as well as stamens, the relative development of the two sets of organs is always so regulated that the stigmas are already perfect and adapted to the reception of pollen at a time when the anthers of the same flowers are still hidden beneath the floral or involucrel envelopes and the pollen is consequently immature. By the time the pollen is completely developed and is in a state to be discharged from the opened anthers, the stigmas of the flower in question are withered and are no longer capable of taking up the pollen. Hence it follows that in these plants the pollen-dust must be transported to other flowers which happen to be at a younger stage of development if fertilization is to be brought about. This is what occurs in nature through the instrumentality of gentle breezes which impose a tremulous motion upon the anthers.

In the first rank of plants belonging to the above category stand the Grasses. Their mode of pollination is so remarkable that it is worth while to look into it a little more closely. One group of Grasses—of which *Avena elatior*, represented in fig. 231, is an excellent example—commences the process under discussion by a sudden distension of the bracts (known by the name of glumes) through the instrumentality of a special turgid tissue situated at their base. The result is that the anthers, till then concealed, are exposed, and it becomes possible for them to be exerted beyond the glumes into the air. This exertion is effected by an extraordinarily rapid longitudinal growth on the part of the filaments. It has been calculated that in some grasses the filiform filaments elongate to the extent of 1–1.5 mm. in the course of a minute, and that usually in ten minutes they are three or four times as long as they were originally. In one subsection of these plants the filaments grow downwards, in another horizontally, and in a third straight upwards towards the sky. The turgidity of the cells in these delicate filaments is so great as to enable even those which grow vertically upwards to support the weight of the anthers without bending. In the case of those Grasses whose stamens grow downwards from the beginning it does no doubt look as though this direction were assumed in consequence of the weight of the anthers. This is not, however, the fact. A high degree of turgidity exists here also, and if one inverts the inflorescences of this kind of Grass, the stamens which have just completed their longitudinal growth remain quite stiff, in spite of their extreme slenderness, and project straight up. Soon after, it is true, this condition ceases. The filaments become slack; those that were erect nod and droop, those that were horizontal fall down, and the anthers are then all suspended at the ends of oscillating threads.

The dehiscence of the anthers is accomplished synchronously with these changes in the filaments. As long as the anthers lay hidden beneath and protected by the glumes they were straight and linear in form (see fig. 231<sup>1</sup>). Each anther consists of two contiguous parallel lobes, and each lobe has a line running longitudinally down it, along which dehiscence takes place. This operation

invariably commences after the anther has assumed a pendent position. The filaments and anthers are joined together by a slender connective, and the tissue of this connective is, as it were, articulated so that the anther is capable of turning freely without becoming detached (a condition termed *versatile*). Hence under any circumstances the requisite position can be assumed; that is to say, the at first uppermost ends of the anthers can be made to hang down whether they are on pendent, or on horizontal, or even on erect filaments. When this inversion has been accomplished the anther-lobes open along the sutural lines already referred to. The slits only gape open for a short distance from that extremity of the anther which is now lowest. This partial opening is in some measure dependent on the further circumstance that at the dehiscent portion the two anther-lobes separate from one another and curve round in opposite directions, as is shown in fig. 231<sup>2</sup>. The significance of this inflection lies in the fact that the powdery pollen is prevented from falling out of the loculi the moment the slits are formed. For the curved ends of the anther-lobes assume the shape of little hollow boats in which the pollen may rest for quite a long time if the air is still (fig. 231<sup>3</sup>). It is not till a gust of wind sets the anthers swinging that the pollen-dust is blown away in the form of a small cloud (fig. 231<sup>4</sup>, to the right). On the first occasion only the tiny heap pertaining to the dehiscent extremity of the anther is removed, but this is immediately replaced by fresh pollen pouring down from the upper indehiscent portion of the anther. This new supply naturally has no long time to wait, but is blown away by the very next gust. The process may be repeated several times, and generally does not cease until there is no longer any pollen left. When the anthers are quite emptied they drop off the filaments in the form of dry husks. Usually, however, this detachment of the anthers does not take place till several hours after pollination, and in the majority of Grasses, plants which have flowered in the early morning or during the day still have their empty anthers hanging to the spikes or panicles, as the case may be, at sunset.

The changes preceding pollination are much more markedly dependent on the weather in Grasses than in other plants. The temperature and hygroscopic condition of the air in particular play an important part. Rain and low temperatures may delay the splitting asunder of the glumes and the extrusion and dehiscence of the anthers not merely for hours, but for days. A very dry atmosphere accompanied by a high temperature also has the effect of retarding the processes above described. The most favourable conditions for pollination in the case of most Grasses prevail in the early morning at an hour when there is still some dew lying on the meadows, when the first rays of sunshine fall obliquely upon the flowers, and the temperature is rising gently and a light breeze sets the spikes and panicles in motion. Under such external conditions as these the phenomena of flowering and pollination are accomplished with astonishing rapidity. In some Grasses an observer may see the glumes relax and spring open, the stamens grow out, the anthers open and the pollen scat-



tered, all in the space of a few minutes. The earliest discharge of pollen begins between 4 and 5 a.m. in the height of summer, and the plants which take part in it thus early are the Meadow-grass (*Poa*), *Kæleria*, and *Avena elatior*. A little later, between 5 and 6 o'clock, comes the turn of the Quaking-grass (*Briza media*) and *Aira cæspitosa*, and of Wheat and Barley (*Triticum*, *Hordeum*). Between 6 and 7 pollination occurs in Rye and in a great number of different Grasses which grow in meadows, such as Cock's-foot-grass (*Dactylis*), *Andropogon*, the Brome-grasses (*Brachypodium*), and many species of Fescue (*Festuca*). Between 7 and 8 o'clock the pollen is liberated from Oats of the *Trisetum* group, from the Fox-tail-grass (*Alopecurus*), Timothy Grass (*Phleum*), and the Sweet Vernal Grass (*Anthoxanthum*). An interval now intervenes, at least amongst the indigenous Grasses. Of exotic species which are cultivated in gardens the following discharge their pollen in the course of the forenoon, viz. the Millets (*Panicum milliaceum* and *Sorghum*) between 8 and 9 o'clock; *Setaria Italica* and the Brazilian Pampas-grass (*Gynerium argenteum*) between 9 and 10 o'clock. Towards noon indigenous Grasses come again into play. About 11 o'clock pollination takes place in most species of the Bent-grass genus (*Agrostis*), and between 12 and 1 in Melic-grass (*Melica*), *Molinia*, Mat-grass (*Nardus*), *Elymus*, *Sclerochloa*, and several species of *Calamagrostis*. In the course of the afternoon the process takes place in a few isolated species, as, for instance, in some Brome-grasses at 2 o'clock, in a few species of Oat (*Avena*) at 3, in *Agropyrum* at 4, and in *Aira flexuosa* between 5 and 6. It is worthy of note that the Soft-grass (*Holcus*), under favourable atmospheric conditions, opens its glumes, pushes forth its anthers, and liberates pollen twice a day, once in the morning at about 6 o'clock, and a second time in the evening at about 7—provided always that the temperature of the air is not less than 14° C. The entire process lasts in most cases from 15 to 20 minutes for each flower.

With the opening back of the glumes and extrusion of the anthers are often connected alterations also in the position and inclination of the stalks which bear the spikelets. For example, the pedicels of the spikelets of *Agrostis*, *Apera*, *Calamagrostis*, *Kæleria*, and *Trisetum* divaricate from the axis, so as to form with it angles of from 45° to 80° for the period of pollination. But as soon as the pollen is discharged all these stalks move back towards the main axis of the inflorescence, and the panicle, as it were, contracts. These movements are obviously designed to give sufficient room to the anthers when they are exerted, in order that they may oscillate freely and so disperse their pollen. In those Grasses where the flowers are crowded together in close spikes, and also in the large *Carex* section of the Cyperaceæ, the bracts do not spring open but only relax, and sometimes merely to such a slight extent that it is scarcely noticeable on cursory inspection. The thread-like filaments are also only partially visible in cases of the kind, the anthers are pushed forward and raised above the glumes through the rapid growth of their filaments. As soon as a filament reaches the proper length its upper

extremity becomes pendulous, and the anther hangs from it and encounters no obstacle to movements such as are required to shake out the pollen.

As in the case of Grasses and Sedges, so also in Hemp and Hops (*Cannabis*, *Humulus*), and in numerous species of Sorrel and Meadow-rue (e.g. *Rumex alpinus* and *R. scutatus*, *Thalictrum alpinum*, *T. fetidum*, *T. minus*) the pollen-dust is shaken out of anthers which are pendulous at the ends of delicate filaments; only,



Fig. 232.—The Elm (*Ulmus campestris*).

1 With flowers.

2 With fruits.

in these plants not glumes but small perianth-leaves form the protective envelope round the anthers before they open. Moreover, in Hemp and Hops, and the above-mentioned species of Meadow-rue, the anther-lobes do not burst wide open when they dehisce, but exhibit parallel slits which are at first so narrow that the pollen can only shake out little by little. Plantains (*Plantago*) also have their pollen shaken out of the anthers, which are borne on long filaments, by the wind. The filaments are tucked in so long as the flower is in bud, but when the petals unfold the filaments straighten out and project beyond the floral spike. The versatile



anthers borne by these filaments are broad and for the most part heart-shaped; the two lobes of which each anther is composed only open on the side turned to the sky,



Fig. 233.—Mountain Pine (*Pinus Pumilio*).

<sup>1</sup> A single polliniferous scale (stamen) seen from above. <sup>2</sup> Three polliniferous scales, one above the other, seen from the side. The pollen falling from each anther alights on the upper surface of the stamen next below. <sup>3</sup> Two spikes of polliniferous scales. <sup>4</sup> Branch with apical group of staminal flowers from which pollen is being discharged. <sup>5</sup> Female flower. 1, 2  $\times 10$ ; 3  $\times 8$ ; 5  $\times 2$ ; 4 natural size.

so that the small gaping slit through which the pollen has to be discharged into the air faces upward. Consistently with this fact we find that in Plantains it takes a couple of days to disperse all the pollen. The same category includes the Elms



(*Ulmus*, see fig. 232), the Japanese *Bocconia* (*Bocconia Japonica*), the Meadow-rues with erect and divergent stamens (*Thalictrum aquilegifolium*, *T. angustifolium*, *T. flavum*, &c.) and several species of *Poterium* and *Sanguisorba*. The filaments of Elms are straight at all times, but they elongate shortly before the anthers open to about double their original length, and the dehiscent anthers are then displayed as pairs of gaping valves. In *Bocconia* the anther-cavities are in the form of long narrow niches, and the erect, radiating, filiform filaments vibrate under the slightest breath of wind like the aigrettes ladies sometimes wear on their heads. In the species of Meadow-rue which grows commonly over the lower Alps (*Thalictrum aquilegifolium*), and in the Siberian Burnet (*Sanguisorba alpina*), the stamens are clavately thickened towards the top, and are organized like those of *Bocconia* in such a manner as to be easily set swinging even when the air is only slightly stirring. The various species of *Plantago*, *Thalictrum*, and *Ulmus* are also remarkable

for the fact that the fissures formed in their anther-lobes during dry weather close up quickly in the event of rain, and remain shut until the rain has ceased and the atmosphere has again become dry.

In all the cases discussed hitherto the pollen escapes from the place where it originates into the air direct. But there are also a large number of plants whose pollen falls in the first instance on to some spot within the province of the flowers, where it is protected from becoming wet, and in which it remains for a period of varying duration; nor is it blown away until conditions favourable to its dispersal obtain in the environment. Very different parts of a flower are utilized in this manner as temporary halting-places for the pollen. In Pines and Firs the backs of polliniferous scales subserve this purpose in a curious way. The upper surface of each anther-scale in the Mountain or Dwarf Pine (*Pinus Pumilio*) is slightly excavated owing to the lateral edges being reflexed and the broad

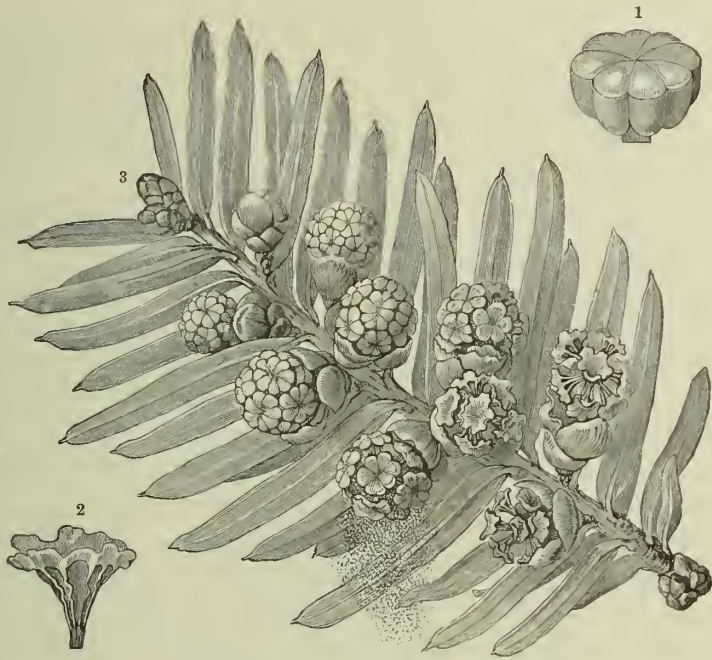


Fig. 234.—Male Flowers of Yew (*Taxus baccata*).

1 Anther with closed pollen-sacs. 2 Anther with its pollen-sacs open and empty. 3 Branch whose lower flowers are discharging their pollen. 1, 2  $\times 2$ ; 3  $\times 7$ .

membranous scale in which the connective terminates being turned up, whilst on either side of the middle line there is a shallow trough (fig. 233<sup>1</sup>). It is easy to convince one's self of the fact that these excavations serve for the reception of the pollen which falls from the anthers above them (see fig. 233<sup>2</sup>), and inasmuch as all the anthers crowded together in a particular spike usually open simultaneously, all the scales of the spike in question have their backs covered with the pollen-dust at the same time (fig. 233<sup>3</sup>). As long as there is no wind the pollen rests on the scales where it has been deposited; but the moment a gust of wind shakes the boughs and twigs of the Pine-tree the pollen is removed from its resting-place, and whole clouds of yellow dust may be seen being blown upward from the spikes (cf. fig. 233<sup>4</sup>).

The corresponding adjustment in the Yew (*Taxus*) differs to a certain extent from the above which is so characteristic of Pines and Firs. The connective of the anther-lobes in *Taxus* does not terminate in an upturned scale, but in a little circular shield with an crenate margin. The anther-lobes are attached to the under surface or back of this shield (see fig. 234<sup>1</sup>). Moreover, the anthers are united into roundish heads, and the peltate connectives lock closely together like the separate parts of a mosaic, so that the pollen-sacs are not visible superficially. When the pollen has reached maturity and has assumed the form of powder, the pollen-sacs concealed underneath the shields burst open, their walls shrivel, and the anthers have then the appearance portrayed in fig. 234<sup>2</sup>. The shields now resemble cupolas, supported by short columns, and arching over spaces in which is stored a heap of loose powdery pollen. Under the influence of a warm, dry atmosphere the tissues of the shields contract somewhat, and in consequence chinks appear between the shields, and the spherical conglomeration of anthers seems to be rent asunder (see fig. 234<sup>3</sup>). When the branches of the Yew are caused to sway by a gust of wind a portion of the pollen is at once blown out through these chinks in the form of a little cloud. In the evening when the atmosphere becomes damper, as also on dull and rainy days, the shields lock together again, and such pollen as is left is once more inclosed and protected from wet. On the return of warm, dry weather the cracks reappear, and the remainder of the pollen may be shaken out and blown away.

The mechanism which has here been described in the case of the Yew, that being an easily accessible example, is found to exist in its main feature, though with many varieties of detail, in the Juniper, in Cypress, and Arbor Vitæ (*Juniperus*, *Cupressus*, *Thuja*). One species of Juniper, viz.: *Juniperus Virginiana*, in which the little heads of stamens are closed when the atmosphere is damp, and open when it is dry, has been already selected for illustration in figs. 226<sup>15, 16, 17, 18</sup>, p. 125. Curiously enough, the Planes (*Platanus*), which are not related to the Conifers just referred to, exhibit similar characteristics in the matter of pollen liberation. The stamens have a peltate or pulvinate connective spread out over the anthers, and each stamen, considered by itself, resembles a short peg or nail with a large, thick head. Besides bearing little papillæ, which are looked upon as abortive

petals, the globular receptacle of the inflorescence supports a large number of these peg-shaped stamens. They stand out in all directions from the sphere, and their peltate connectives have their edges in contact as in the case of the Yew. Similarly, also, cavities are formed beneath the roof, composed of the connectives, and serve as temporary resting-places for the pollen-cells when they are discharged



Fig. 235.—Hazel (*Corylus Avellana*) with flowers and fruits.

from the dehiscent and shrivelling anthers. The final process of dispersal of the pollen in the form of dust is, however, essentially different from that which occurs in Yew, Cypressess, and Junipers. In Planes individual stamens fall out of the spherical inflorescence, like bits out of a mosaic, and thus gaps are formed which constitute the means of egress from the cavities filled with pollen-dust. The inflorescences are suspended by long stalks, like big beads on a knotted string, and



as soon as a wind sets them in motion the pollen is discharged through the gaps in little clouds.

A temporary deposition of the pollen on the backs of the flowers is common to all the numerous trees and shrubs which have their male flowers aggregated in pendent catkins or spikes resembling tassels or fringes in appearance, as, for instance, the Hazel (*Corylus*, see fig. 235), the Alder (*Alnus*, see fig. 228), the Walnut (*Juglans*, see vol. i. p. 742), Birches, Poplars, and Hornbeams. The floral spikes of all these plants are erect at first, and in the form of short, thick cones



Fig. 236.—Curled Pondweed *Potamogeton crispus*) in the act of pollination.

and cylinders. A short time before the anthers burst the axis of the spike elongates and becomes pendent, causing all the flowers seated upon it to assume an inverted position with their originally upper faces turned to the ground and their backs upwards. The back of each flower is so contrived as to catch the pollen falling from the anthers of the flowers above it, and retain it until the tassels are set swinging by a gust of wind, and the pollen is in consequence dissipated (*cf.* vol. i. p. 741).

Sometimes the hollow upper surfaces of sepals, petals, or bracts serve as landing-stages for the pollen when it is discharged. This is the case, for example, in various species of the Pondweed genus (*Potamogeton*), in the Arrow-grass (*Triglochin*), and the Sea-Buckthorn (*Hippophae*). In the Curled Pondweed (*Potamogeton crispus*), a plant which lives submerged in ponds and slow running

brooks, and in the height of summer raises its flower-spikes above the surface of the water (see fig. 236), the large, fleshy, reddish-brown stigmas are already ripe to receive the pollen at a time when the anthers close beside them are still closed. The perianth-leaves of the flowers concerned are indeed still folded together, and may be seen underneath the four projecting stigmatic lobes which are arranged in a cross, whilst the anthers are hidden beneath the perianth. The shortly-stalked, concave perianth-leaves do not open back until the stigmas have begun to wither. Almost at the same instant longitudinal slits are formed down the large, white anthers, and they are speedily converted into gaping fissures, out of which flows a copious supply of yellow pollen of mealy consistency. If a fresh, dry wind is blowing at the moment of the dehiscence of the anthers part of the pollen is at once carried off from the spikes of the Pondweed as they project above the water; but if a calm prevails a certain amount of the pollen drops into the cavity of the particular perianth-leaf immediately below the anthers. Here the pollen may remain for hours together if there is no wind. It is only blown away by a strong puff of wind, and is then conveyed directly to other spikes projecting out of the water whose flowers happen to be in a much earlier stage of development, the four radiating stigmatic lobes being in a receptive condition, but the anthers yet indehiscent and the perianth-leaves still closed (see fig. 236).

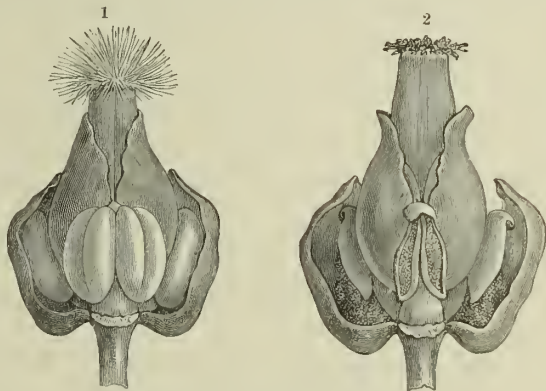


Fig. 237. —Arrow-grass (*Triglochin palustre*).

<sup>1</sup> A flower with brush-like stigma already mature; all the anthers still closed. <sup>2</sup> A flower with the stigma withered whilst the three inferior anthers have opened and are depositing their pollen in the concave perianth-leaves at their bases. In both flowers the lower front perianth-leaf has been cut off.  $\times 8$ .

A still more striking instance of the temporary storage of pollen in concave perianth-leaves is found in the Arrow-grass (*Triglochin*). Here, too, the development of the stigmas precedes that of the anthers by two or three days. During the whole period that the brush-like stigma at the top of the ovary is sound and in a receptive condition the anthers are closed, and they only open when the stigmas have faded and turned brown (*cf.* figs. 237<sup>1</sup> and 237<sup>2</sup>). The stamens, six in number, are in two whorls of three each, situated one above the other (*cf.* vol. i. p. 646), and underneath each stamen there is a deeply-concave perianth-leaf. As soon as the anther opens the pollen rolls into the receptacle thus prepared beneath it, whilst in the meantime the perianth-leaf has moved a little away from the axis and somewhat loosened its connection with it. The pollen rests in its hollow until a puff of wind sets the slender floral spikes swaying to and fro and blows away the pollen. It is a noteworthy circumstance that all six anthers of a flower do not open at once, but that first the lower whorl of stamens comes into play, and that after their pollen has been carried away

by the wind as above described both the empty stamens and the perianth-leaves at their bases drop off. Only after this has happened does the upper whorl of perianth-leaves relax; the anthers of the three upper stamens burst open, their pollen glides into the bowl-shaped perianth-leaves below, and exactly the same process is repeated as took place in the case of the superior whorls.

The case of the Sea-Buckthorn (*Hippophae*; cf. figs. 220<sup>2, 3, 4, 5</sup>, p. 109), is worth mentioning as a third example of the same nature. The flowers of this shrub are conglomerated in little tufts on the sides of woody branches. Each male flower is composed of four stamens and two opposite concave scales; the latter have their edges in contact, so that they form a little bladder within which the four stamens are concealed. The pollen is of an orange-yellow colour and mealy consistency, and is set free from the anthers at a time when the bladder is still closed. It falls into the cavity, and is there completely sheltered from rain and dew by the overarching scales. When a warm, dry wind sweeps over the shrubs the bladders open by two opposite chinks, and the pollen is blown out from its resting-place in small quantities at a time. In damp weather the two scales close up quickly and protect what remains of the pollen from wet; on the return of dry weather they move apart again, leaving a free passage for the wind, which then carries off the rest of the pollen. This simple mechanism ensures the safety of the pollen in the event of rain, whilst enabling it to reach the stigmas of neighbouring shrubs whenever the external conditions are propitious.

A close connection exists between these various contrivances to ensure that pollination shall only take place at the best possible moments, and the maintenance of a free passage in the direction in which the pollen is to be transported by the wind, and further between these adaptations and the shape of the stigmas devised for the reception of the pollen. It is obvious that no barrier must be interposed in the path of the little clouds of pollen-dust on their journey to the stigmas. If the flowers of the Arrow-grass, of Pondweeds, or Grasses were wrapped in large foliage-leaves a great part of the pollen would adhere to these leaves and would be as irretrievably wasted as if it had fallen to the ground or into the water. On this account also all flowers which have their pollen blown out of them by the wind are arranged in spikes and panicles at the upper extremities of the shoots and project freely into the air, but are never clothed with a mass of foliage. Particular attention may be drawn to the fact that a large number of plants wherein the pollen is in the form of dust flower before coming into leaf; that is to say, yield up their pollen to the wind at a time when the green foliage is still folded up in the buds or is just emerging from them. The Sea-Buckthorn, the Alder, the Ash, the Elm, the Hazel, the Birch, and the Aspen all flower and discharge their pollen at a season when the branches are bare of leaves (cf. the illustrations on pp. 109, 135, 138, 143, and 147). Were these plants to begin to blossom after the complete development of their extensive foliage the wind-transport of the pollen would be rendered



almost impossible. The way to the stigmas would be stopped by innumerable barriers, and the pollen would inevitably be deposited upon these obstacles and stranded.

As regards the stigmas, we find that in plants with dusty pollen they are invariably fashioned so as to catch the dust. In one case they are fleshy and swollen and have the surfaces which are exposed to the wind covered with a velvety coating (see fig. 236), in another they are in the form of tufts of long papillose or capillary filaments, as, for instance, in the Paper Mulberry-tree (*cf.* figs. 229<sup>1</sup> and 229<sup>6</sup>, p. 137); sometimes they assume the shape of delicate feathers (*cf.* fig. 231, p. 139), sometimes of camel's-hair pencils and brushes (fig. 237). At the time when pollination takes place they are always fully exposed to the wind and so placed that when the pollen-cells are blown against them they are caught like midges in a spider's web. Yet, in spite of all these contrivances, it would remain very doubtful whether the stigmas would be dusted with pollen through the action of wind were it not for the concurrence of another circumstance. The wind is but an uncertain means of transport, especially in the case of a passive object incapable of exercising any influence on the selection of a route. It is, therefore, important that the pollen should be disseminated broadcast in as thorough a manner as possible, and this is only possible if the number of pollen-cells is excessively large. Supposing that only two thousand pollen-cells were produced in a Nettle-inflorescence and these were surrendered to be the sport of the wind, it would be only by a lucky chance that a single one of these cells would be caught by the stigmas of a plant at a distance of 5 metres; but, inasmuch as the number of the cells constituting the pollen-dust of a Nettle amounts to millions, the probability of successful pollination is increased to a proportionate extent. If the stamiferous flowers of Conifers, Hazels, Birches, Hemp, or Nettles be picked before the dehiscence of their anthers and placed on a suitable substratum until the anthers open, the mass of pollen-dust which is liberated is quite astonishing. It seems scarcely credible that so large a quantity of pollen could have been developed in anthers which are themselves so small, and the apparent anomaly only becomes intelligible when one remembers that the cells were packed closely together in the anthers, but afterwards lie simply in a loose heap. In years peculiarly favourable to the flowering of Conifers vast clouds of pollen are borne on gentle winds through the Pine-forests, and are often swept right beyond them, so that not only the female flowers, needles, and branches of the trees in question are powdered over with the yellow pollen, but also the leaves of adjoining trees and even the grasses and herbs of the meadows around. In the event of a thunder-shower at such a period the pollen may be washed off the plants and run together by the water as it flows over the ground, and then, after the water has run off, streaks and patches of a yellow powder are left behind on the earth, a phenomenon which has given rise on various occasions to the statement that a fall of sulphurous rain has taken place.

## DISPERSION OF POLLEN BY ANIMALS.

If this book were ornamented with pictorial initial letters illustrative of the contents of each section, we should have at the head of this chapter a group of flowers with bees and butterflies swarming round them, whilst into the scrolls of the capital would be woven a representation of the quiet life of field and forest as manifested on bright summer days—a subject which plays a prominent part in the poetic descriptions and pictorial art of all unsophisticated nations. Even in these days, pictures of butterflies fluttering about bright-coloured flowers, or of bees engaged in collecting the materials for their honey-combs, still find an appreciative public. Young people especially take pleasure in subjects of the kind, and, since youth never entirely dies out, there will always be people who prefer to see the beautiful lines and tints of flowering meadow and shady wood depicted in miniature than the bold outlines of a landscape. If, however, mere casual observation of the relations between flowers and their insect visitors is sufficient to cause æsthetic pleasure, and has stimulated people of every age and nationality to the production of works of art, it may be imagined how great must be the incentive to scientific study supplied by a deeper insight into these phenomena, and what extreme pleasure is derived from the successful discovery of the reasons for these wonderful relations, and from tracing their connection with other facts of science. It may be confidently asserted that the careful investigation of the processes connected with the visits paid by insects and other animals to flowers has brought the solution of the main problems of modern science considerably nearer, and we have good ground for hoping that the prosecution of these researches will succeed before long in raising the veil which still conceals the truth in the case of a number of unexplained phenomena.

Zoologists are quite justified in their assertion that many of the developments of insects' bodies are correlated with the forms of particular flowers. But equally true is the conclusion to which botanists have arrived that many of the properties of flowers are likewise in correlation with the shape and habits of flower-seeking insects. Now, these flower-loving animals which would perish if for a single year the earth were destitute of blossoms, vary to an extreme degree in size and shape, in the nature of their external coatings, in what they require for nutrition, and in respect of their time of flight, and of a large number of other habits dictated by soil and climate. From the tiny midges to humming-birds, from the thrips, which are scarcely 1 mm. long, and live and die with the flowers, to the gigantic butterflies of Ceylon, Brazil, and New Guinea, whose expanded wings measure 16 cm. across, and which flutter cumbrously from flower to flower, a long and graduated series extends which corresponds with a perfectly similar series in the floral world. The diversities of colour in the creatures which visit flowers, the various kinds of mechanism of flight exhibited by beetles, flies, bees, butterflies and birds, the multiplicity of organs by means of which they extract their food from

the flowers, their means of attachment to the blossoms, their fur and bristles for brushing off the pollen, have all their corresponding variations in form and colouring amongst flowers, and consequently there is an equally long and apparently parallel series in the realm of plants.

Contemporaneously with the opening of the earliest spring flowers occurs the escape of the first pioneer butterflies from their cocoons; the same sunny day which rouses hive-bees and humble-bees from their winter sleep, sees the Willow-catkins protrude from their brown bud-scales and offer their honey and pollen to the world at large. Many flowers which open early in the morning are only visited by particular butterflies which forsake their nocturnal haunts at the same hour; as soon as the flowers close at sunset the insects in question also seek their quarters, fold their wings, and remain the whole night fast asleep. Other flowers do not open till sunset, when day-flying butterflies are already gone to rest, and they are visited by Hawk-moths, Silk-moths, Owlet-moths, and other Noctuæ which have remained throughout the day concealed in shady nooks and commence their ramblings when dusk sets in. These instances of the mutual relations existing amongst vital phenomena obtrude themselves annually on the notice of the most superficial observer, and have been described time after time.

We need not occupy ourselves any longer at the present day with an account of the facts themselves, but rather with the inquiry into the causes both proximate and remote of all phenomena which are presented to our wondering senses. First of all, the question arises: what is it that induces insects and small birds to visit flowers, and what advantage accrues to a plant from the visits with which its flowers are favoured? The answer is, that the inducement is in some cases care of young, in others the desirability of securing themselves against dangers from storms, and, most commonly of all, it is the craving for food. Flowers, however, do not provide animals with breeding-places, with temporary shelter, or suitable nutriment without claiming a reciprocal service, but have their parts so adjusted that their visitors become laden with pollen, which is then transported to other flowers and deposited on their stigmas where it initiates a series of changes resulting in the setting of the seeds. The next few pages will be devoted to the elucidation and proof of this general answer by aid of individual instances.

As regards the choice of nests for their young it has long been known that the nocturnal Lepidoptera of the genus *Dianthæcia*, and also some species of the genus *Mamestra* lay their eggs in the flowers of Caryophyllaceous plants, *e.g.*, in those of the Nottingham Catchfly, the Bladder-campion, Ragged Robin, and Common Soapwort (*Silene nutans*, *Silene inflata*, *Lychnis Flos-cuculi*, *Saponaria officinalis*). The eggs, which are brought forth through a comparatively long ovipositor, produce tiny caterpillars which move about freely in the undivided cavity of the ovary, and there enjoy not only complete shelter but suitable nutriment, for they live on the ovules and young seeds which are seated upon the central placenta situated in the middle of the ovary. When they grow up they bite a hole in the side wall of the ovary, creep through it and descend to the ground, where they pass into the



chrysalis condition. One may see, frequently, on examining the ripe fruit-capsules of the Catchflies, the perforations by which the moth-larvæ have gained their freedom. If the caterpillars of *Dianthæcia* devoured all the seeds in the ovaries, the species of plants frequented by them would derive no benefit, but, on the contrary, an injury from their visits. Owing to the large number of ovules, however, they are very seldom completely destroyed, and even if all the seeds in one of the capsules were to be consumed there would always be other capsules in the same plant which would develop plenty of seeds capable of germination. The majority of the Caryophyllaceous species here in question, the Nottingham Catchfly (*Silene nutans*, see figs. 238 and 239) amongst the rest, flower at night, their blossoms

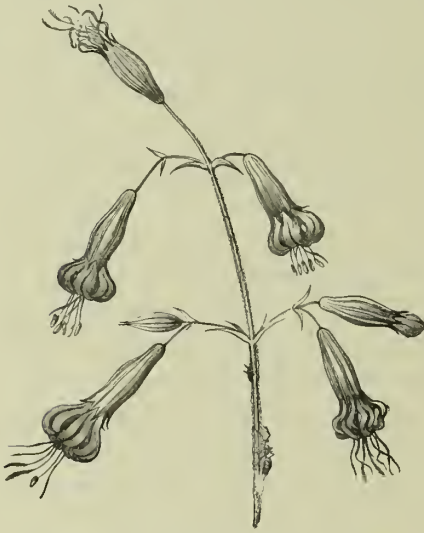


Fig. 238.—The Nottingham Catchfly (*Silene nutans*) in the daytime.

opening at dusk, remaining expanded all night, and closing at sunrise. This is repeated in the case of each flower at least three times. On the first evening the petals which have hitherto been rolled up and folded in the bud, spread themselves out in rays and bend somewhat back (fig. 239); five anthers are rapidly exerted from the middle of the flower, and these soon afterwards dehisce, become covered with adhesive pollen, and remain the whole night in that condition. In the course of the following morning the filiform filaments bearing the anthers belonging to the outer circle of stamens bend back, and the anthers fall off or, less commonly, are left hanging to the ends of the reflexed filaments in the form of empty shrivelled sacs. The next evening

the second whorl of stamens included in these flowers comes into play, and just in the same manner as before, five anthers, which dehisce at nightfall, are exerted from the mouth of the flower and expose their pollen. The third day these stamens likewise bend back and usually let their anthers drop, and when dusk sets in the long velvety S-shaped stigmas, which have till then been concealed inside the flower, are pushed out. Certain changes of position affecting the petals proceed simultaneously with these mutations. It has already been mentioned that the petals rolled up in the bud unfold on the first night, and assume a stellate and reflexed attitude. At this time also the flowers emit a delicate perfume like that of hyacinths, which attracts a large number of nocturnal insects, but only lasts from 8 o'clock in the evening till about 3 A.M. At daybreak the petals begin to roll up again, the operation taking place faster when the temperature is moderately high and the sky clear than when the weather is cold and the sky overcast. In the process of involution the petals fall into longitudinal folds and become wrinkled and grooved, so that they hang like five crumpled bags round the mouth of the flower, and

by their appearance might lead one to think that the flower had faded (see fig. 238). But as evening approaches the wrinkles vanish, the petals unfold, spread themselves out into a star, and become slightly reflexed once more. One peculiarity of these flowers is that the inner surface of the petals is white, whilst the outer surface is always of some inconspicuous colour, such as dirty-yellow, greenish, brown, dull red, or ashen-grey. Hence the radiating petals with their white inner surfaces exposed are very striking in the evening darkness, whereas in the daytime the crumpled petals with only their backs visible are anything but conspicuous, and give the impression of being already brown and withered, as may be seen in fig. 238. They are consequently not noticed by insects in the daytime and receive no visits from them.

This appears to be exactly what is aimed at. Such insects as visit flowers by day in order to suck their honey would be the reverse of welcome to the Catchfly. The filaments are reflexed, the anthers shrivelled and empty or dropped, and there is no pollen in the flower to be brushed off. A honey-sucking insect could not either take up or deposit pollen in the daytime, and the honey would therefore be sacrificed in vain. Indeed, the flowers would be worse off inasmuch as, being despoiled of their honey, they would possess one less means of attraction in the ensuing night. On the approach of night the pollen-laden anthers and velvety stigmas appear in front



Fig. 239.—The Nottingham Catchfly (*Silene nutans*) by night, a flower being visited by the moth *Dianthæcia albimacula*.

of the entrance to the interior of the flower where the honey is concealed, the scent and white colour act as allurements, and the visits of insects are welcome, provided the size of their bodies is such that they rub against the pollen or stigmas and fly quickly from one flower to another. Those which are too small, or are destitute of wings, are still kept at a distance, this being effected by means of contrivances which will be the subject of discussion later on. Of all the welcome species the best adapted in respect of size and shape of body, length of proboscis, and various other structural characteristics are the Owlet Moths (*Noctuæ*), and of these in particular those of the genus *Dianthæcia*, one of which is represented as visiting the flower of the Nottingham Catchfly in fig. 239. These little moths pay frequent visits to suck the honey whilst the females also lay their eggs in the flowers. It sometimes happens, too, that the females become loaded with pollen from a flower upon which they have rested and taken a meal of honey, and that afterwards they fly with the pollen to other flowers where, instead of sucking any more honey, they

lay their eggs, and in so doing dust the stigmas with their freight. To sum up, the flowers of the Nottingham Catchfly and of other species of Caryophyllaceæ above referred to are adapted to the small Noctuæ of the genera *Dianthæcia* and *Mamestra*, and are visited exclusively, or, at any rate, principally, by those insects. The Noctuæ obtain honey from them, and the females find in them homes suitable for their eggs. The return made by the moths to the plants consists in the conveyance of pollen from flower to flower and the consequent conversion of ovules into seeds which would not be effected spontaneously.

The relations just described occur also among several other groups of plants and Lepidoptera. A number of species of the small blue butterflies belonging to the genus *Polyommatus* stand in the same relation to Leguminosæ and Rosaceæ. The beautiful *Polyommatus Hylas* visits the flowers of Lady's-fingers (*Anthyllis Vulneraria*) and in doing so transfers the pollen from one plant to another. The female lays her eggs in the ovaries of the flowers she visits, and from the eggs issue caterpillars which feed on the young seeds. When mature the caterpillars forsake the ovaries and retire underground to pass through the chrysalis stage. The same relation exists between *Polyommatus Baticus* of Southern Europe and the Bladder-Senna (*Colutea arborescens*), between *Polyommatus Arcas* and the Great Burnet (*Sanguisorba officinalis*) and in many other cases; only, besides the butterflies named, others alight with a freight of pollen on the flowers of these plants, but do not lay eggs in the ovaries, and only receive honey in return for their conveyance of the pollen, so that these cases are really only partially of the same category.

On the other hand, the life-history of one of the moths living on the capsule-bearing species of the genus *Yucca*, and named *Pronuba yuccasella*, has been made out, and must here be dealt with in some detail, as it affords one of the most wonderful examples of the dispersal of pollen by means of egg-laying insects. The flowers in all species of *Yucca* are arranged in large panicles (vol. i. fig. 154, p. 659), and each is bell-shaped and suspended at the end of a smooth, green stalk. The perianth-leaves, six in number, are yellowish-white and are consequently visible from a considerable distance in the dusk and on moonlight and starry nights. After the flower-buds open, which happens regularly in the evening, the perianth forms a widely-open bell (*cf.* fig. 240<sup>1</sup>). The dehiscence of the small anthers, which are supported on thick and velvety filaments, takes place simultaneously with the divergence of the petals, and a golden-yellow adhesive pollen is to be seen in the spiral slits of the anthers. Each flower is wide open for one night only; by the next day the free extremities of the six perianth-leaves bend towards one another causing the flower to assume the form of a balloon or bladder with six narrow lateral apertures (fig. 240<sup>1</sup>). In the twilight and by night, numerous small yellowish-white moths (*Pronuba yuccasella*; see fig. 240<sup>4</sup>) which have a metallic glitter in the moonlight flutter about the flowers of the *Yucca* plants. The females penetrate into the interior of the wide-open bells and there endeavour to possess themselves of the pollen, not with a view to devouring it, but that they may carry it away. For this purpose they are furnished with a special implement. The first



joint of the maxillary palp is lengthened to an extraordinary extent, and its inner surface is beset with stiff bristles and can be rolled up like a trunk (see fig. 240<sup>5</sup>). It is used to seize the pollen, to conglomerate it into a ball and afterwards to hold



Fig. 240.—Transport of Pollen by Egg-laying Insects.

- <sup>1</sup> Branch from the inflorescence of *Yucca Whipplei*; the middle flower open, that beneath it was open the previous night and is now closed again, the rest of the flowers in bud. <sup>2</sup> Single flower of the same plant visited by a moth of the species *Pronuba yuccasella*; the three front perianth-leaves removed. <sup>3</sup> Stigma of *Yucca Whipplei*. <sup>4</sup> *Pronuba yuccasella* flying to a flower of *Yucca Whipplei*. <sup>5</sup> Head of *Pronuba yuccasella* with a ball of pollen held by the coiled maxillary palp. <sup>6</sup> Twig with inflorescence of *Ficus pumila*; the urn-shaped inflorescence (or synconium) cut through longitudinally. <sup>7</sup> Single female flower from the bottom of the synconium of *Ficus pumila*. <sup>8, 9</sup> Stamens of the same plant from the upper part of the synconium. <sup>10</sup> Synconium of *Ficus Carica* full of gall-flowers produced by *Blastophaga*, cut through longitudinally; near the mouth of the cavity is a Fig-wasp (*Blastophaga grossorum*) which has escaped from one of the galls. <sup>11</sup> Synconium of *Ficus Carica* full of female flowers, cut through longitudinally; near the mouth of the cavity are two Fig-wasps, one of which has already crept into the cavity whilst the second is about to do so. <sup>12</sup> Male flower. <sup>13</sup> Long-styled female flowers of *Ficus Carica*. <sup>14</sup> Gall produced from a short-styled gall-flower. <sup>15</sup> *Blastophaga grossorum* escaping from a gall. <sup>16</sup> A liberated *Blastophaga*. <sup>17</sup> The same magnified. 1, 2, 4, 6, 10, 11, 16, natural size; <sup>3</sup>  $\times 2$ ; <sup>5</sup>  $\times 20$ ; <sup>7, 8, 9, 12, 13</sup>  $\times 5$ ; <sup>14, 15, 17</sup>  $\times 8$ .

it. In a very short time a moth collects by its means a ball of pollen, which is held by the rolled-up palpi close underneath the head and resembles a great crop. Laden with this lump of pollen, which is sometimes three times as large as its head, the

moth abandons the despoiled flower and seeks another forthwith. Having found one, it circles nimbly round it, making a sudden spring off and on, and ends by settling on two of the thick reflexed filaments, sprawling its legs out upon them. It then seeks to reach a favourable spot on the surface of the pistil with its ovipositor and there deposits its eggs. The ovipositor is composed of four horny bristles, and is adapted to pierce through the tissue of the pistil. After the eggs are laid and the ovipositor is withdrawn, the moth darts to the top of the infundibuliform stigma (fig. 240<sup>3</sup>), unrolls its trunk-like palpi, and stuffs the pollen into the stigmatic funnel, moving its head to and fro repeatedly during the operation (fig. 240<sup>2</sup>). It is alleged that the same moth repeats the processes of alternately laying eggs and stuffing the stigma with pollen several times in the case of the same flower.

Most of the eggs introduced into the pistil are deposited in the vicinity of the ovules. They are of oblong shape, narrow and transparent and increase rapidly in size, soon revealing in each a coiled-up embryo. On the fourth or fifth day the larva is hatched and at once begins to devour the ovules in the cavity of the ovary. Each grub requires from 18 to 20 ovules to nourish it during the period of its development. When it is grown up, it bites a hole in the still succulent wall of the ovary, crawls out through the aperture, lets itself down to the ground by a thread, burrows into the earth and spins an oval cocoon underground in which it remains till the following summer. Fourteen days before the time of flowering of the *Yucca*, it begins to show signs of life, and the moment the flowers of that plant open the silvery moths escape from their pupal envelopes.

An important element in the interpretation of the relations subsisting between the *Yucca* and the *Yucca*-moth is the fact that without the assistance of insects the sticky pollen of the plant in question could not get to the stigma. In the case of *Yucca aloefolia* alone there seems to be sometimes a transfer of pollen to the stigma through the instrumentality of the petals or of the elongating filaments; but in most species of this genus, that is to say, in those wherein the fruit is capsular, this certainly does not take place. With the exception of the moth referred to, insects but seldom fly to them, and those which alight by chance on the flowers do not cause a deposition of pollen on the stigmas. If it were not for the transport of the pollen by *Pronuba yuccasella* the ovaries and ovules of *Yucca* would not ripen into fruits and seeds. As a matter of fact, all the fruits of the capsular species are rendered abortive if moths are kept away from the flowers by means of a gauze covering. Also, in gardens where there are no *Yucca*-moths, the production of fruit is suppressed. *Yucca Whipplei*, which in California, its native land, is visited by a particular moth and develops an abundance of dehiscent capsular fruits, has repeatedly flowered in the Botanic Gardens of Vienna, but the moth does not exist in the gardens, and, in consequence of its absence, not a single fruit has ever ripened there. On the other hand, it is ascertained beyond a doubt that the grub of the moth in question lives exclusively on the young seeds of these species of *Yucca*, so that one is forced to the conclusion that the moth stuffs the



pollen into the stigma in order that its grubs may be supplied with the nutriment requisite for the preservation of the species—nutriment which would not be forthcoming unless the ovules were fertilized.

This inference does not, of course, involve the assumption that the operations in question are carried out deliberately by the moth with an intelligent foresight of the results. But there is no objection to our looking upon the habits of these insects as unconsciously purposeful. The stuffing of the pollen into the stigmatic funnels is neither more nor less wonderful than the fact that in remote valleys where the population is very sparse and there are very few vegetable gardens, the cabbage white butterfly often flies miles away to look for cabbages upon which it may lay its eggs so that the grubs may find the food that suits them the moment they are hatched. Equally marvellous, too, is the case of many kinds of caterpillar which spin their cocoons on the bark of trees, and cover the structures wherein they are subsequently to undergo transformation into the chrysalis-state with lichens and fragments of bark, that their temporary resting-place may not be noticed by insectivorous birds; and again the same sort of phenomenon encounters us in the case of the caterpillars which live in the interior of the hard parts of plants, and before transforming themselves into pupæ make a special exit ready for the soft and delicate imago subsequently to be liberated.

It must be observed that the grubs of *Pronuba yuccasella* do not eat up all the developing seeds of the ovary in which the moth lays her eggs. There are about 200 ovules in each ovary. Even if half or two-thirds of them are consumed, there is still a sufficient number of uninjured seeds left to be scattered abroad when they have reached maturity, whereas without the intervention of the moth not a single seed capable of germination would have been produced. Whether or not symbiosis with moths also occurs in the species of *Yucca* bearing berries has not been ascertained for certain; but seeing that the berry-producing species, *Yucca aloefolia*, *Y. Treculeana*, &c., have been found to have holes in all their mature fruits—at least when they are growing in their native countries (Florida, Carolina, Mexico, Louisiana, Texas)—and other traces have been discovered pointing to their having been occupied by caterpillars, the probability is very strong that such is the fact.

Still more remarkable than the relation between the genus *Yucca* and its companion moth is that existing between Fig-trees and certain small wasps of the group of the Chalcididæ. To understand the relation clearly, it is first of all necessary to examine the construction of the inflorescence in the Fig. Looking at a fig that has been cut open lengthwise, as is shown in fig. 240<sup>6</sup>, it is observed that it is not a simple flower, but rather a whole collection of flowers inclosed in an urn or pear-shaped receptacle. These pear-shaped shoots are in reality hollow inflorescences bearing numerous flowers on their inner walls. Each fig is termed a synconium. The orifice of the urn is very small, and is further straitened by the presence of small leafy scales. The flowers, which are very simple in structure, almost fill the entire cavity; they are of two kinds, male and female.



Each male flower is composed of one or two—rarely from three to six—stamens, which are supported by scales, and are borne on a short stalk (fig. 240<sup>12</sup>). In many species, as, for instance, in *Ficus pumila*, the stamens are spoon-shaped and have the anthers imbedded in the concavity of the spoon (figs. 240<sup>8</sup> and 240<sup>9</sup>). The female flowers possess a unilocular ovary containing a single ovule. The style is inserted rather to one side of the ovary and terminates in a stigma, which is variously formed. At the base of the ovary are to be seen a few small scales which vary in number, and may be regarded as the perianth (see figs. 240<sup>7</sup> and 240<sup>13</sup>). Many species have two kinds of female flower in the same urn or synconium, viz. some with long styles and developed stigmas, and some with shorter styles and abortive stigmas. The latter are called gall-flowers for a reason that will presently be explained (fig. 240<sup>14</sup>). The relative distribution of male and female flowers is very different in different species. In the inflorescences of the India-rubber Fig (*Ficus elastica*), figured on p. 755, vol. i., the male and female flowers are apparently mixed together promiscuously; in that of *Ficus pumila* (fig. 240<sup>6</sup>) female flowers only are found in the lower part of the cavity, and only male flowers near the mouth. This distribution is the most usual, but yet another difference exists in respect of the number of male flowers. In the synconia of many species the male flowers occur in large numbers near the orifice, whilst in others there are very few—indeed it even happens sometimes that there is an entire absence of male flowers in one inflorescence or another. In many species some individuals only produce inflorescences containing female flowers, and other individuals inflorescences with male flowers near the orifice and with female flowers lower down. But the most remarkable circumstance of all is that in the inflorescences of many species all or most of the female flowers below the male ones are transformed into gall-flowers. This is the case, for instance, in the common Fig-tree (*Ficus Carica*) cultivated in Southern Europe, a species which includes two kinds of individuals, viz. those whose inflorescences contain female flowers only, and those whose inflorescences contain male flowers near the opening and gall-flowers lower down (*cf.* figs. 240<sup>10</sup> and 240<sup>11</sup>). The former individuals are known by the name of *Ficus*, the latter by the name of *Caprificus*.

We have now to consider what may be the meaning of the gall-flowers. As the name indicates, not fruits but galls are produced from these modified female flowers, and this happens in the following manner. There is a small wasp belonging to the Chalcididæ, a family of Hymenoptera (*cf.* fig. 240<sup>16</sup> and 240<sup>17</sup>), already referred to as *Blastophaga grossorum*, which lives upon the Fig cultivated in the south of Europe. This insect passes into the cavity of the inflorescence through the orifice, and there sinks its ovipositor right down the style-canal of a flower, and deposits an egg close to the nucellus of the ovule. The white larva developed from the egg increases rapidly in size and soon fills the entire ovary whilst the ovule perishes. The ovary has now become a gall (fig. 240<sup>14</sup>). When the wasps are mature they forsake the galls. The wingless males are the first to emerge, and they effect their escape through a hole which they bite in the gall. The females remain a little

longer in their galls and are there fertilized by the males. Afterwards they come out also (*cf.* fig. 240<sup>15</sup>), but only stay a short time within the cavity of the inflorescence, issuing from it as soon as possible into the open air. They accordingly crawl up to the mouth of the inflorescence, and in doing so they come into contact with the pollen of the male flowers and get dusted all over the body—head, thorax, abdomen, legs, and wings. After squeezing through between the scaly leaves at the mouth of the inflorescence, and having at last reached the outside, they let their wings dry and then run off to other inflorescences on the same or on a neighbouring Fig-tree. I say “run” advisedly, for they but rarely make any use of their wings in this act of locomotion. They now seek exclusively inflorescences which are in an earlier stage of development, that they may lay their eggs in the ovaries. Having found such an one they crawl to the opening and slip between the scales into the interior. Sometimes their wings are injured in the act of entering, indeed, the wings are occasionally broken off altogether, and are left sticking between the scales near the aperture.

Once inside the inflorescence, the wasps immediately devote themselves to laying eggs, and in the process are of necessity brought into contact with the stigmas of female flowers. The wasps are still powdered over with the pollen from their birthplace, and it is now brushed off on to the stigmas, which are thus pollinated from another inflorescence. If the pollen is deposited on normal pistilliferous flowers the latter are able to develop seeds endowed with the power of germination; if it falls on gall-flowers it is, as a rule, ineffectual, because the stigmas are more or less abortive. Moreover, no seeds are formed in these gall-flowers, owing to the eggs of the wasp being laid in their place. In those species of Fig in which gall-flowers are not specially provided, the eggs are laid in a certain proportion of the normally-developed female flowers. It has, however, been observed in the case of the Common Fig (*Ficus Carica*) that eggs of *Blastophaga grossorum* laid in ordinary female flowers do not come to maturity, or, in other words, that a normal female flower is not converted into a gall, even if the wasp in question sinks its ovipositor into it and deposits an egg in the interior. For the style of the normal female flower of *Ficus Carica* (fig. 240<sup>13</sup>) is so long relatively to the ovipositor of *Blastophaga grossorum* that the egg cannot be inserted quite into the ovary, but is left at a spot which is not favourable to its further development and there perishes. The gall-flowers of this species of Fig, with their short styles (fig. 240<sup>14</sup>), are, on the other hand, pre-eminently adapted to the reception of the egg at the spot where the ovule would otherwise develop, whilst at the same time they are not adapted to the production of seeds capable of germination, since no pollen-tubes can develop upon their abortive stigmas. Evidently we have here a case of complementary functions or division of labour in accordance with the following plan. The wasps which deposit their eggs in the figs carry the pollen both to the short-styled gall-flowers and to the long-styled ordinary female flowers, and attempt to lay their eggs in both kinds of flower. The gall-flowers are prepared expressly for the reception of the wasps' eggs, and young wasps actually develop in them; but their

stigmas not being adapted to the reception of pollen they do not promote the growth of pollen-tubes, and no fertile seeds are produced. On the other hand, pollen-tubes develop on the stigmas of the long-styled flowers, and the latter produce fertile seeds; but the long-style prevents the proper placing of the wasps' eggs, and consequently galls are never or very seldom produced in connection with these flowers.

It would take too long to discuss all the numerous diversities which have been observed in other species of Fig, even if they were known with sufficient accuracy to admit of a general survey. We will only mention that there are approximately 600 species of *Ficus*, which are distributed over the tropical and sub-tropical regions of both the Old and the New Worlds, and that up to the present time nearly 50 species of small wasps of the genera *Blastophaga*, *Crossogaster*, *Sycophaga*, and *Tetrapus* have been identified as effecting the transference of pollen from one inflorescence to another in the various species of Fig. Thus, for instance, *Blastophaga Brasiliensis* has been identified in the inflorescences of seven different kinds of Fig-tree. For the most part each species of Fig has its own particular wasp; only in extremely rare instances have two different species of wasp been found in the inflorescences of one and the same species of Fig.

In Southern Italy and other parts of Southern Europe where the Fig has been extensively cultivated for ages, the majority of the trees planted are *Ficus*-individuals, *i.e.* such as have female flowers only in their inflorescences, these yielding the best and juiciest figs. Fig-plants of the form known as *Caprificus*, which, besides male flowers, contain only gall-flowers in their inflorescences, are not cultivated, because most of their figs dry up and fall off prematurely. A few specimens of *Caprificus* are reared here and there in order that their inflorescences may be artificially transferred to the branches of the *Ficus*-trees. The process of transference is called *caprification*, and the growers believe that the figs of *Ficus* are improved by the wasps which come out of the *Caprificus*-inflorescences and enter those of the *Ficus*. But this opinion, though very wide-spread amongst cultivators and peasants, is not correct. The figs of *Ficus* do not require the intervention of wasps to become sweet and juicy. As a matter of fact, *Ficus*-inflorescences which have been entirely unvisited by wasps and have developed no fertile seeds in their little fruits, ripen into excellent eating figs, and innumerable quantities of the figs sold come from trees and from districts where no process of caprification is employed. It seems, therefore, that the use of caprification must be traditional and have originated at a time when growers were not only concerned with the production of good fruit but of fertile seeds also with a view to the multiplication of the plants. At the present day Fig-trees are no longer raised from seed but from cuttings, and caprification is consequently superfluous. Nevertheless the country people persevere with the old custom in spite of their ignorance of its real significance.

Flowers and floral envelopes are comparatively seldom called upon to act merely as a shelter for the night, or as a temporary refuge. Most bees and wasps have



their own homes which are furnished with safe retreats, and to these they withdraw at dusk and in bad weather, and butterflies, for the most part, are afraid to seek the interior of flower-bells or funnels for any length of residence partly because of their relatively large wings, which are liable to be injured in such confined quarters, and partly because in case of danger a rapid escape from the inside of a flower would be scarcely possible. Only beetles, flies, and Hymenoptera of the genera *Meligethes*, *Melanostoma*, *Empis*, *Andrena*, *Cilissa*, and *Halictus* need be mentioned; they are essentially nomadic in their habits, not possessing homes of their own or any settled night-quarters, but are satisfied with second-rate shelter, and usually pass the night wherever they have spent the day. If there should happen to be flowers there which offer agreeable food in addition to a warm retreat so much the better. Doubtless it is for these reasons that the honey-bearing blossoms of the Bell-flowers (*Campanula*) and the Foxglove, the interiors of which after sundown have a somewhat higher temperature than the environment (cf. vol. i. p. 500), are especially favourite shelters on cold nights. The large capitula of *Crepis grandiflora*, and of several other Composites whose outer ligulate flowers close in the evening, are also sought after by small beetles (*Cryptocephalus violaceus*, *Meligethes æneus*) and little dark-coloured bees (*Panurgus ursinus*) to serve as nocturnal refuges, because a higher temperature prevails at night inside the closed capitula than outside. At sunrise they abandon their night-quarters, and in doing so probably—in some cases inevitably—brush off some of the pollen which they carry away and take with them on subsequent visits to other flowers.

Sometimes insects remain in comfortable quarters of the kind not only during the night but also during the day, and even for several days. When once the small beetles of the genera *Anthobium*, *Dasytes*, and *Meligethes* have ensconced themselves in the interior of the flowers of Magnolias or Gentians (*Magnolia obovata*, *M. Yulan*, *Gentiana acaulis*, *G. ciliata*, *G. Pneumonanthe*, &c.), they do not abandon this comfortable home till the third day. This is also true of the rose-chafers (*Cetonia*), which have a preference for the flowers of *Magnolia grandiflora*. They usually force themselves into the youngest flowers which are only just open and take their fill of the sweet juices exuding on and between the stigmas. Later on they devour also some of the pollen as it is liberated from the anthers and drops upon the petals. When the Magnolia-flowers open under a bright mid-day sun, the Cetonias keep still and warm themselves in the sunshine, and when evening comes, and the upper petals close up, they have no inducement to leave the quarters they have chosen, for the temperature rises in the inclosed space during the night from five to ten degrees Centigrade above the temperature outside, and, besides, the Cetonias are here completely sheltered from the attacks of nocturnal animals. Thus they stay in the flowers until the petals fall off and leave them exposed to the air. The flowers of the Opium Poppy (*Papaver somniferum*) are likewise sought out by flies and beetles as soon as they open, and are not deserted until the petals drop. The sojourn is, however, much shorter than in the case of Magnolia-flowers owing to the fact that the Poppy only closes once for the night and loses its petals the very next day.

In the examples above referred to the insects are not forcibly retained in the flowers, for in fine weather the flowers of Gentians, Magnolias and Poppies are as



Fig. 241.—*Arum conocephaloides*, with the front wall of the spathe removed. On the lowest part of the spadix are the female flowers, above them the first ring of bristles, next the male flowers, and then a second ring of bristles. At the bottom of the cavity are a number of midges belonging to the genus *Ceratopogon* whose escape is prevented by the stiff deflexed points of the lower ring of bristles.

wide open as they can be. But there are also cases where insects, after slipping into a floral cavity for shelter, are kept there for a time imprisoned. This remarkable phenomenon is exhibited especially by the Aroideæ and Aristolochiaceæ. In many Aroideæ (*Arum*, *Dracunculus*, *Helicodiceros*, &c.), of which *Arum conocephaloides* (fig. 241) may be taken as a type, the ensheathing spathe widens out above, whilst below the middle there is a decided constriction, and the lowest part expands into a barrel-shaped receptacle. The temperature inside the cavity is always considerably above that of the environment, and ranges not infrequently from 30° to 36° C.; in the spathes of the Italian *Arum* (*Arum Italicum*) a temperature of 44° C. has even been recorded (see vol. i. p. 501). All these Aroideæ have an offensive odour of putrefaction, and by this very property attract a number of animals which live on dead bodies and other decaying matter. These creatures settle on the projecting end of the spadix and climb down it into the barrel-shaped cavity, where they find a warm habitation and in addition a supply of food in the thin-walled succulent cells lining the interior. At the part where the spathe is constricted the spadix is encompassed by a ring of stiff bristles, which form a contrivance like a lobster-trap. The points of most of the bristles are curved downwards, so as to allow the insects to climb down into the chamber but prevent their egress. It is not till some days later that the bristles become limp, the constriction in the spathe is loosened and expanded, and the captives are able to leave their temporary prison, and by that time the pollen has been liberated from the anthers and covers that region of the spadix which bears the male flowers; it is thus impossible for insects to climb up the spadix without first becoming loaded with the pollen lying in their way, and they afterwards carry it to other younger flowers. In *Arum conocephaloides* (fig. 241) there are two rings of bristles, one above the other.

The upper hairs relax later than the lower ones, and when, after the latter have

become flaccid, midges that have been imprisoned at the bottom of the cavity pass into the upper story, they are kept there for a time by the upper bristles, which are still rigid, so that the insects knock against the male flowers and must cover themselves with pollen. Finally, when this object is achieved, the upper bristles also relax and the midges are allowed to escape.

It is astonishing what a large number of insects and what a variety of different kinds find a home in the flowers of Aroideæ. The smaller Aroids, such as *Arum maculatum*, widely distributed in Europe, are sought chiefly by tiny midges of the species *Psychoda phallænoides*, and it is not uncommon to find several hundreds of them in the cavity of a single spathe. In the receptacle formed by the spathe of an *Arum conocephaloides*, planted in the Botanic Gardens of Vienna, three species of small black midges of the genus *Ceratopogon* had congregated, and were present in such large numbers that when one of the spathes was opened artificially a whole swarm flew out. A second spathe of the same plant, which was immersed in alcohol and subsequently opened, was found to contain nearly a thousand midges of the kind. In the Italian *Arum* (*Arum Italicum*) also as many as sixteen different species of flies, mostly of the genera *Chironomus*, *Limosina*, *Sciara*, and *Psychoda*, have been found in a single spathe. Another Aroid, *Dracunculus crinitus*, is sought principally by large flies belonging to the species named *Somomyia Cæsar* and *Anthomyia scalaris*. In the receptacles formed by the spathes of the *Dracunculus Creticus*, which has flowered in the Botanic Gardens of Vienna, various carrion-beetles (*Aleochara fuscipes*, *Dermestes undulatus*, *Saprinus nitidulus*, &c.) had collected, besides numerous green-gilded flies of the genera *Anthomyia*, *Lucilia*, and *Somomyia*; and in the sheathing-bracts of *Dracunculus vulgaris* which grows in Italy scarcely anything but carrion-beetles of the genera *Dermestes* and *Saprinus* have been observed. A single spathe of the last-named plant was once found to contain more than 250 carrion-beetles belonging to eleven different species.

The flowers of the Birthwort genus (*Aristolochia*) bear a surprising resemblance to the spathes of Aroideæ, their perianths being, like aroid spathes, divided into three regions. First of all, there is the limb, which in the European species has the form of a trumpet, and in the tropical species of America assumes many other curious shapes, as, for instance, that exhibited by *Aristolochia ringens* (fig. 242), where it is drawn out into a boat-shaped under-lip with an upper-lip arching over it. Next comes a tubular median portion, which is furnished with various contrivances to prevent the egress whilst permitting the entrance of creatures seeking shelter. Lastly, there is an enlarged basal portion like a bladder or pouch wherein the stigma and anthers are situated, and which constitutes the goal of the insect-visitors. On a future occasion it will be necessary to enter more fully into the manner in which the insects that creep into the pouch take up and afterwards deposit the pollen, and it will therefore be sufficient to mention here that they are kept prisoners there until the anthers have opened. When dehiscence has taken place, and not before, the tubular middle region undergoes certain changes which make it possible for the captives to escape from their temporary dungeon.



For flowers to serve as refuges and nocturnal haunts for insects they need not necessarily be fashioned into hollow receptacles, pouches, bells, or anything of the kind, as is proved by the following observation. In my garden the flowers of plants of *Phlox paniculata*, indigenous to North America, and of the Canadian Golden-rod (*Solidago Canadensis*), which bloom simultaneously in the autumn, were visited by numberless flies—particularly by the large bee-like *Eristalis arbus-*

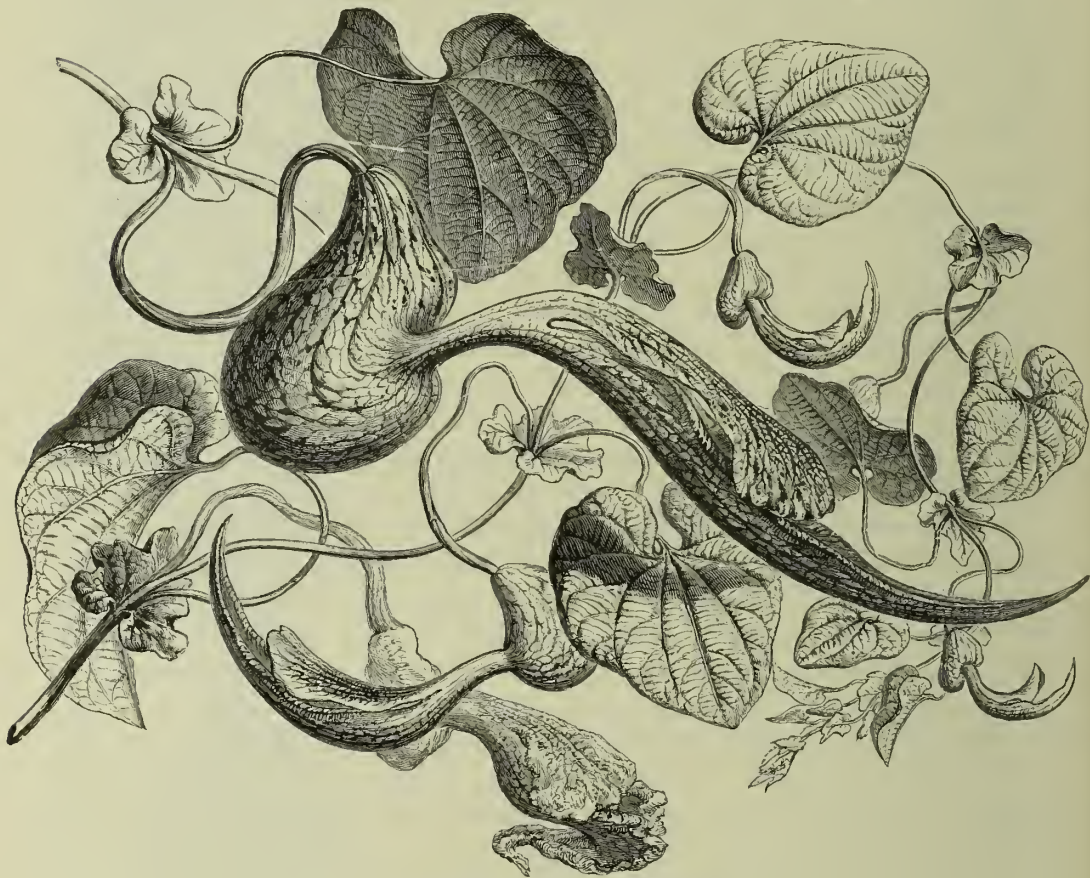


Fig. 242. — *Aristolochia ringens*. (After Baillon.)

*torum*—which feasted on as much of the pollen as was accessible to them. By day they stayed as readily on the Phlox-flowers as on the Golden-rod; but as night approached they one and all migrated to the Golden-rod. Not a single fly remained on the Phlox, whereas the great bunches of Golden-rod capitula were covered with hundreds of flies. On the following night, which was still and cold, I examined the flowers by the light of a lantern and found that less dew was deposited on the flowers of the Golden-rod than on those of the Phlox, and this led me to conjecture that the temperature of the former flowers had risen in the night above that of the surrounding atmosphere. And this turned out to be the case. A thermometer inserted in the middle of the inflorescence of the Golden-rod,

which was in full flower, recorded a temperature about  $2^{\circ}$  higher than the environment, and probably there would have been a still greater difference if the form and disposition of the capitula had not been peculiarly unfavourable to the retention of the warm layer of air in immediate contact with the flowers. The inflorescences of the Phlox exhibited no rise of temperature, but, on the contrary, a fall of  $1.5^{\circ}$  as compared with the surrounding atmosphere, and they were copiously bedewed. Thus the flies had selected a relatively warm place for their night's rest, although it could not really be called a shelter. As the pollen in the Golden-rod is pushed during the night out of the tube formed by the anthers, the flies found on awaking next morning their meal again ready for them, and it was evidently impossible that they should leave their nocturnal resting-place without first smearing themselves over with pollen.

#### ALLUREMENTS OF ANIMALS WITH A VIEW TO THE DISPERSION OF POLLEN.

Next to honey pollen is the principal food which animals seek for in flowers. There are some plants from which honey is entirely absent, and which offer only pollen to the food-seeking animals. Such, for example, are the Poppy (*Papaver*), Traveller's Joy (*Clematis Vitalba*), Pheasant's Eye (*Adonis*), and several Anemones (*Anemone alpina*, *baldensis*, *sylvestris*, *Hepatica*, &c.), the numerous Cistuses and Rock-roses (*Cistus* and *Helianthemum*), and Roses (*Rosa*). They all agree in this: that their flowers when open stand erect and have a star-shaped or cup-like form, so that the pollen falling out of the anthers is not lost, but remains for some time on the concave upper surface of the petals. This is especially noticeable in flowers of the Poppy family (*Eschscholtzia*, *Glaucium*, *Roemeria*, *Argemone*; cf. fig. 222<sup>1</sup> p. 112, and fig. 243). In comparison with the honey-producing flowers, to be described later on, they always appear to have a simpler construction, which is accounted for by the fact that they have no need of special contrivances for the secretion and storing or protection of honey.

The flowers of these plants are eagerly sought for by little beetles of the genera *Anthobium*, *Dasytes* and *Meligethes*, and it is no uncommon thing to find in a single *Cistus* or Rock-rose flower, half a dozen *Dasytes* greedily devouring the pollen. Along with the beetles numerous flies also visit these honeyless flowers for the sake of the pollen, more especially certain Ruscidæ, Stratiomyidæ, and Syrphidæ, which seize the pollen-cells with the terminal lobes of their mouth-parts, bruise them thoroughly, and swallow them bit by bit. Besides these, certain Hymenoptera, e.g. species of *Prosopis*, and also Thrips (*Thrips*), are eaters of pollen, and if they establish themselves in great numbers can in a short time almost entirely clear away all there is to be found.

It is well known that bees and humble-bees collect pollen in large quantities and carry it to their nests as food for the larvæ. The collecting is carried on by means of specially constructed hairs and bristles, which clothe various parts of the body, particularly the abdomen and the terminal segments of the hind-legs, and



which are sometimes found united into a thick fur, sometimes arranged in regular rows or bands, or grouped into brushes. Some of the hairs are soft and flexible, like delicate little feathers, and when these structures are crowded close together, they act just like a dusting-brush. The pollen over which they have swept, and with which they have become covered, remains hanging between the feathers, from which it can easily be removed afterwards. Other hairs, as already mentioned, are short and stiff, and resemble eyelashes or bristles, arranging themselves in regular rows, so as to form small besoms. In bees and humble-bees these brushes occur on the end-segments of both hind-legs, while in species of *Osmia* only a single brush is formed on the lower side of the abdomen. When these insects stroke the pollen-covered anthers, or the petals on which the loose pollen has fallen, with their legs



Fig. 243.—Honeyless Flower of *Argemone Mexicana* with abundant pollen.

or abdomen, they remove the pollen with the small brushes and the chinks between the bristles are quite filled with it. Moreover, the bees and humble-bees, with the assistance of the brushes on the terminal segments of their hind-legs, are able to comb and sweep off the pollen which was imprisoned in the soft hairs of their own fur, and thus these brushes form excellent collecting apparatus. In addition, these insects have special contrivances on their legs which have been compared to little baskets; they are smooth, sharply-defined hollows, hedged in by stiff rod-like bristles, in which the pollen, pressed

into clumps and pellets, is packed up to be carried home. Many of these Hymenoptera moisten the pollen which they wish to collect with honey-juice, especially if it is powdery or dust-like, so as to be able to knead it into the little baskets. For instance, when the bees wish to obtain the pollen of the Plantain (*Plantago*) as it emerges from the clefts of the anthers, they eject on it first of all some honey from their extended sucking-tube, by which means the loose mass becomes coherent and adapted for collection. It also frequently happens that the loose pollen to be collected is already provided with juices from the perforated, turgid tissue of the neighbouring petals. If the pollen is sticky provision of this kind is not needed. The slightest disturbance and the most delicate touch are then sufficient, and the pollen adheres to the body of the insect, even the smooth hairless parts of the thorax, the abdomen, and the legs being covered with it.

Since the sole use of insect-visits to flowers is the transference of the pollen from one flower to another, it is evident that some restriction must be placed upon its too extensive demolition. As a great part of the pollen can always be eaten in the flower, or carried off to the nest as food for the larvæ, it is necessary that some should remain adhering to the body of the visitor, so that the stigmas of other flowers may be adequately provided. This necessity is excellently met by the



superfluity of pollen. All flowers which contain no honey and offer only pollen as food for the insects, *e.g.* those of Cistuses and Roses, of Poppies and Clematises are characterized by a large number of stamens containing so much pollen that in spite of the extensive depredations of the insects, the necessity of pollinating the stigmas is always provided for. The pollen-eating beetles, after visiting such flowers, are always powdered all over with pollen, and as they cannot immediately rid themselves of that which clings to their thorax, abdomen, wing-cases, and legs, when they leave the flowers, they invariably carry it to other flowers. The bees and humble-bees also, which enter such flowers to collect pollen, come out covered as if with flour, and when subsequently they set to work energetically with their leg-brushes to clear the dust from their fur, there always remains behind enough to give the stigmas of other flowers their portion when they next visit them.

Flowers which conceal honey in their depths are very economical with their pollen, and in them care has been taken that it shall not be squandered or uselessly scattered. Animals which frequent flowers poor in pollen are, moreover, vigorous honey-suckers and do not attempt either to eat the pollen or to collect and carry it into the nest for their brood. Involuntarily, they become streaked and clothed with pollen, a state of affairs not always agreeable to them. At the same time it cannot be very disagreeable, for the animals may be seen immediately after flying out of the pollen-strewing flowers as if frightened, entering flowers of the same species in the next moment where they will experience the same treatment. It would indeed be strange if the same flowers should on the one hand have such contrivances as will allure insects in order that they may transfer the pollen from plant to plant, and on the other hand be so arranged as to shock these laden and attracted guests, and disincline them to further visits. Such a contradiction never does occur in the flower-world, but all the contrivances connected with the transference of pollen display a harmony which fills those who busy themselves with these phenomena with astonishment and admiration.

The dusty, flour-like coatings which are observed on the flowers of some Orchids, particularly of the genera *Eleanthus* and *Polystachya*, are very similar to pollen in outward appearance, but in reality wholly different. They consist of masses of loose, round cells which lie in rows like necklaces of pearls on the upper side of the young petals. As a rule, this covering occurs only on the unpaired leaf of the Orchid-flower known as the lip, which thus resembles a tiny cup filled with flour. The loose cells, which look like flour or dust, contain starch, sugar, oil, and albuminous compounds, and so form an excellent food, serving, just like the pollen-cells, to allure and please the insects.

For the most part these dusty, flour-like coatings are rare. It more frequently happens that rows and masses of cells which project from the surface of certain parts of the flower, appearing to the unaided eye as papillæ, hairs, swellings, and warts, are offered as food to these flower-visiting insects, and must therefore be reckoned so far as allurements. In the flowers of the *Portulaca* (*Portulaca oleracea*) there is a ring-shaped cushion covering the spherical ovary, from its inner

edge spring the stamens, and from its outer margin the petals. Between these two floral whorls the fleshy cushion is seen to be beset with clear, diaphanous papillæ, which, indeed, secrete no juice, but are nevertheless sucked by small insects visiting the flowers, and are sometimes actually eaten. The same is true of the delicate hairs which beset the staminal filaments of the Pimpernel, Mullein, and Spiderwort (*Anagallis*, *Verbascum*, *Tradescantia*), and which under the microscope appear to be turgid cells arranged singly or in rows just like the hairs which clothe the bottom of the hollow perianth-leaf in the flower of the Lady's-Slipper Orchid (*Cypripedium*). In several species of the genus *Lysimachia* (*Lysimachia thyrsiflora*, *ciliata*, &c.), the ovary is covered with small warts whose juicy cells are sucked or devoured by animals; and in the flowers of the Snowflake (*Leucojum*



Fig. 244.—Flowers of the Snowflake (*Leucojum vernum*).

<sup>1</sup> Seen from the side. <sup>2</sup> The front part of the flower cut away and the remaining part of the perianth spread out in one plane. Round the style is a cushion of soft tissue which secretes no honey. (Both figures somewhat magnified.)

*vernum*; cf. fig. 244), there is a cushion-like mass of cells surrounding the style, whose significance is identical with that of the small warts just mentioned. Numerous Orchids, too, viz. *Odontoglossum*, *Oncidium*, and *Stanhopea*, bear fleshy swellings, pegs, and combs on their perianths which admit of a similar interpretation.

It also often happens that certain portions of flat petals consist of a cell-tissue which can be easily perforated and sucked by the mouth-apparatus of insects. Such parts are usually distinguished from their surroundings by their greater brilliancy, and one might suppose that this was due to a thin layer of fluid, although this is not really the case. Especially noticeable in this respect are the flowers of *Centunculus minimus*, a tiny Primulaceous plant, whose cup-shaped corolla is carpeted at the bottom with slightly-arched, large, juicy, superficial cells, which glitter like silver in the sun. The petals of the Bloodwort (*Sanguinaria*), of the St. John's Wort (*Hypericum*), of the Laburnum (*Cytisus Laburnum*), of *Spartium*, and of many other plants, behave in the same way. Repeated observations have also shown that the petals of Hyacinths and of many Anemones, and the flowers of the Centaury (*Erythraea*), as well as the hollow, honeyless spurs of our

meadow Orchids (*Orchis mascula*, *militaris*, *Morio*, &c.), are pierced and sucked by insects, and it should be noted here that not only flies, bees, and humble-bees, but even butterflies are capable of boring into juicy tissue. Butterflies have at the end of their maxillary laminæ which compose their proboscis, certain sharp-pointed appendages with which they first rip up the juicy tissue and then steal the liquid.

A special allurement to those insects which are accustomed to pierce and suck juicy tissues is observed in species of *Eremurus* (*E. altaicus*, *caucasicus*, *tauricus*), indigenous in Altai, Caucasus, and Taurus. These plants, which belong to the Liliaceæ, bear a raceme on a long rachis which elongates greatly during flowering. When the flower-buds open the petals are spread out flat, and surround the still closed anthers like a six-rayed star. This only lasts for a short time. As soon as the anthers dehisce and expose their sticky, orange-coloured pollen, the petals roll themselves up, become shrivelled, and form a small dirty red-brown ball, from which spring six thick greenish swellings. These swellings, which are really the juicy veins of the under sides of the petals, resemble green aphides. The fly *Syrphus pirastræ*, which is known to seek for Aphides, pierces and sucks these swellings, apparently mistaking them for the insects; at any rate they pierce the rolled-up flowers of *Eremurus* just like Aphides, and, what is most wonderful about the matter, they load themselves by this means with the pollen of the anthers standing in front of the flower, and convey it to the stigmas of other flowers.

We shall have to speak presently of plants whose flowers are only open for a day, a night, sometimes only a few hours. The petals of these plants have this peculiarity, that when they wither they fall quickly, become discoloured, crumpled or rolled up, and pulpy. Then the cell-sap exudes from the tissue and covers the surface with a thin layer of fluid. Pulpy petals of this kind are visited by insects, specially by flies, which lick up and suck the juice, and at the same time cover the stigma with pollen brought from other flowers. This is the case, for example, in *Calandrinia*, *Tradescantia*, and *Villarsia*. This proceeding is an uncommon one, for the simple reason that the number of plants with such short-lived flowers is very limited.

On the other hand, the secretion of juices on the surfaces of fresh tissues of flowers that remain open several days is a widely-spread phenomenon, so that it is perhaps not too much to say that this secretion occurs in 90 per cent of flowers visited by insects and humming-birds. The secreted juice contains more or less sugar and has a sweet taste. But along with the sugar there are also various other ingredients in solution. According to the variable contents of these ingredients the consistency, the colour, and the smell of the liquid of course vary considerably. Sometimes it is watery and colourless, while at other times it is a thick fluid and brown like treacle. The dark liquid, as it is found in the flowers of *Melianthus*, has an unpleasant and even an offensive odour. But in most cases the smell is similar to that of bees' honey. For the most part this sweet sap is practically the same as honey, and this name is therefore now given to it by most botanists.



Botanists of earlier time called it nectar, and those parts of the flower which prepared and stored it, when they were readily distinguishable, were called nectaries.

The secretion of honey takes place in many cases through stomata, and these are either distributed uniformly over the surface of the tissue, or collected together in particular spots. Usually the stomata are large and of the form known as water-pores. In the Willows (*Salix*) the peg-like or tabular nectary bears only a single large water-pore at its truncated end, which pours out colourless honey. There are also nectaries which are quite devoid of stomata and in which the sweet juice comes to light by diffusion through the outer walls of the superficial cells. Sometimes the inner layer of this cell-wall seems to break down into mucilage, becomes changed into a gummy substance, then into sugar, finally pouring out from clefts in the cuticle which has been raised up like a bladder and burst.

The amount of the honey secreted varies very much. In many plants the drops exuding from the stomata of the petals are so small as to be scarcely visible to the naked eye. In others the honey forms an extremely thin layer, looking as if the tissue had been stroked over with a moist brush. In most cases the small drops flow together into larger drops, which fill the grooves, cylinders, depressions, and cups prepared for their reception. Sometimes these receptacles become filled to overflowing, and then at the least touch the sweet juice flows out of the flowers in drops. This occurs, for example, in *Melianthus major*, growing at the Cape, from whose flowers, with their large cowl-shaped honey-receptacles, an actual rain of honey pours when the inflorescence is shaken. So much fluid honey is secreted by two small horn-like processes in the flower of a tropical Orchid named *Coryanthes*, that it continues to flow for a long time from the points of the horns. The lower end of the so-called lip is hollowed out, and gradually the cavity is quite filled by the trickling honey. The quantity of sweet fluid which so collects amounts to about 30 grammes.

In most instances the most important ingredient of the honey for alluring insects, viz. sugar, is in solution, both on account of its chemical properties and also because the sweet fluid in the hidden grooves and tubes of a flower is thus less exposed to evaporation. Sugar crystals of considerable size formed from the sweet juices of the flower are only found in some Orchids of the genus *Aerides*. It is not necessary to do more than allude to the fact that, as well as in flowers, the sugary solution which pours out from the bracts of certain Composites becomes changed into crumbly crystalline masses, though it may be deserving of short notice. Of this form of sugar as a much-desired food of ants we shall speak in a subsequent chapter.

Usually the honey remains exactly where it has been formed and excreted, but there are some flowers in which this is not so; *i.e.* those where the sweet juice flows from its place of origin and is stored up in special receptacles or honey-bags. This, for example, is the case in the flowers of *Coryanthes*, *Melianthus*, *Viola*, and *Linaria*. It has already been mentioned that in *Coryanthes* there exists an actual collecting-cup, which receives all the honey as it trickles

down from the horn-shaped secreting bodies. In *Melianthus* there are two narrow petals from which the honey drops into the cup-shaped sepal. In *Viola* each of the two lower stamens is furnished with a long process which projects from the connective, and these processes excrete honey, which trickles down into the expansion of the lower, middle petal surrounding them. In the Toad-flax (*Linaria*) the honey is excreted by a cushion at the base of the ovary, but flows from it through a narrow cleft between the two longer stamens into the hollow spur of the corolla directed downwards and backwards.

In addition to portions of the flower proper, bracts can secrete honey. In many flowers single members only are changed into nectaries, but in others a whole whorl of members. Tissue-bodies are often seen which are difficult to explain from the standpoint of speculative morphology, because of the incomplete knowledge of their development, and of which it is impossible to say whether they have arisen directly from the receptacle or from a leaf-structure. On this account it is also not easy to classify or enumerate nectaries in a thoroughly satisfactory manner. If, therefore, in the following a certain order is observed, this is only for the sake of distinctness, and not with the idea that the structures placed side by side belong necessarily to one and the same morphological category.

In the flowers of most Umbelliferous Plants, of the Cornel, Ivy, Golden Saxifrage, of numerous species of Saxifrage and Spindle-tree (e.g. *Euonymus europæus*, cf. fig. 245<sup>1</sup>), a cushion of tissue is developed on the ovary. The stamens and floral-leaves stand round this cushion in a circle but not so as to conceal it, and in the open flower within the corolla the honey may be seen glittering in the sunshine like a thin coat of varnish. The middle of the shallow, basin-shaped flowers of the Sumach (*Rhus*), of the Buckthorn (*Rhamnus*), and of the Red Currant (*Ribes*, cf. fig. 245<sup>2</sup>) is covered with a fleshy disc which secretes fluid honey over its whole surface. The Box (*Buxus*) exhibits in the middle of both its staminate and pistillate flowers three little swellings meeting together, each of which deposits a drop of honey. In the Lady's Mantle (*Alchemilla*), *Sibbaldia*, and *Scleranthus* the flower is divided into two stories, into a lower cup-shaped, in which stands the ovary, and an upper, shallower one formed by the floral-leaves. Between the stories is a disc perforated in the middle, or rather a flat ring is interposed which may be compared to the diaphragm in the tube of a microscope. This band also glistens on its upper side in consequence of an extremely thin layer of honey spread over it. The honey-secreting tissue of the Spurge (*Euphorbia*) is very peculiar. The thickly-crowded flowers are surrounded by a cup-shaped envelope



Fig. 245.—Honey-secreting tissue in flowers.

1 Flower of the Spindle-tree (*Euonymus europæus*);  $\times 4$ . 2 Flower of the Red Currant (*Ribes rubrum*) cut through longitudinally;  $\times 5$ .

whose edge is studded with crescent-shaped, oval, or rounded bodies. These bodies glisten on their upper side with a thin coating of nectar, just like the cushions on the ovaries of Umbelliferous Plants or of the Spindle-tree.

In the flowers of the Sloe, Almond, and Peach trees, Raspberries and Strawberries, some Cinquefoils, and numerous other Rosaceæ, a fleshy tissue is formed around the ovary or its summit, which, spreading from the base of the flower, lines the calyx-tube like a vestment (*cf.* fig. 246<sup>1</sup>). This tissue secretes honey which, however, is not visible from the exterior, because of the very numerous stamens

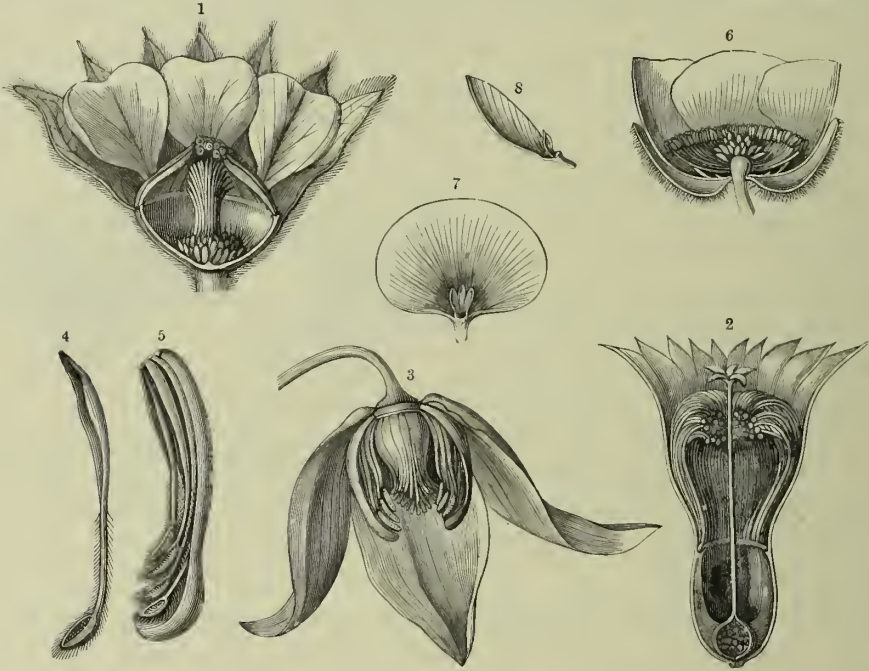


Fig. 246.—Nectaries.

<sup>1</sup> Flower of Cinquefoil (*Potentilla micrantha*), the front part cut away. <sup>2</sup> Flower of *Mammillaria glochidiata*, the front part cut away. <sup>3</sup> Flower of *Atragene alpina*, the front part cut away. <sup>4</sup> Stamen of the *Atragene* with trough-like filament (anther downwards). <sup>5</sup> Four imbricating trough-like stamens of the same plant held together by a spoon-shaped petal. <sup>6</sup> Flower of *Ranunculus glacialis*, the front part cut away. <sup>7</sup> A single petal of the same, seen from above. <sup>8</sup> The petal cut through longitudinally, seen from the side. <sup>3</sup>, <sup>4</sup>, <sup>7</sup>, <sup>8</sup> natural size; the other figs. somewhat enlarged.

which surround it and roof it over. In the flowers of Cactuses, also, the lowest cup-shaped or tubular portion is covered inside with a honey-secreting layer of tissue (*cf.* fig. 246<sup>2</sup> showing *Mammillaria*).

In the Thymelaceæ, Scrophulariaceæ, Gesneraceæ, Boraginaceæ, and Labiatae the honey-tissue forms a wall surrounding the base of the ovary like a ring; while in the closely-allied Rhinanthaceæ, particularly in the genera *Bartsia*, *Clandestina*, *Lathræa*, and *Pedicularis*, there is a cushion which is attached to only one side of the base of the ovary, and in *Rhinanthus* and *Melampyrum* at the same point a fleshy, honey-secreting lobe. Moreover, in the Cruciferae, the tissue surrounding the stalk of the ovary is thickened and swollen, while warts and pegs which secrete honey project from it here and there. In the Stocks (*Matthiola annua* and



*incana*), in *Alyssum*, *Schiverekia*, and *Thlaspi* such warts are seen right and left of the two short stamens, and in *Alliaria* and *Draba* one wart projects from the longer pair of stamens from the outer side facing the corolla. It must remain uncertain whether these structures are to be regarded as part of the stem or as metamorphosed leaves. In many cases—as, for example, in *Haberlea*, *Pæderota*, and *Polemonium*, where the ring-shaped cushion is divided into five, and in *Scrophularia*, where it is divided into two symmetrically-placed lobes—the appearance is in favour of the latter view. In the flowers of the Bindweeds (*Convolvulaceæ*) the base of the ovary is surrounded by five thick honey-secreting scales of equal size, which together form a small cup reminding one of an egg in an egg-cup, and in the *Crassulaceæ* a little knob or a fleshy scale projects from the circular wall of the base of the flower opposite each carpel, sometimes spoon-shaped (*Sedum annuum*), sometimes linear and split at the free end (*Sedum atratum*), and of other varied forms. In these instances the honey-secreting structures are without doubt to be regarded as metamorphosed leaves.

Instances are comparatively rare where the formation of honey is carried on by the carpels—as, for example, the flowers of several *Primulaceæ* (*Androsace*, *Aretia*), in which the slightly arched roof of the ovary secretes minute drops of nectar, and in those of many *Gentians* (*Gentiana acaulis*, *asclepiadea*, *Bavarica*, *Pneumonanthe*, *prostrata*, *punctata*, &c.), where the bulb-like, thickened base of the ovary exhibits five cushions which exude abundant honey into the base of the flower-tube. In the flowers of some *Liliaceæ* and *Melanthaceæ* (e.g. *Albuca*, *Ornithogalum*, *Tofieldia*), the honey is secreted in the lateral grooves of the ovary, and in the flowers of *Anthericum* as well as of *Allium Chamæmoly* a small depression is found on each of the three lines of union of the carpels from which a drop of honey is poured.

Nectaries are found much more frequently on the stamens. They occur there in all sizes and shapes. Sometimes it happens that whole stamens are changed into nectaries, which of course can only be at the expense of the anthers. The stamens of the Whortleberry and Bog-whortleberry (*Vaccinium Myrtillus* and *uliginosum*), like those of Tulips (*Tulipa*), have a small depression which secretes honey on the broad thickened base of the filament opposite the corolla. In the widely-distributed Meadow Saffron (*Colchicum autumnale*) there is an orange-coloured honey-secreting body on the stamens just above the place of union with the violet leaves of the perianth, and the honey there formed fills a channel which traverses the adjoining perianth-leaf. The same thing occurs in other Saffrons and also in the genus *Trillium*. In Geraniaceous plants, especially in *Erodium* and *Geranium*, a wart-shaped, sometimes hollow, nectary arises on the base of each of the five inner stamen-filaments on the side directed towards the sepals. The nectaries at the base of the thread-like filaments of many *Caryophyllaceæ* exhibit an immense variety of form. Sometimes all the stamens of a flower are a little thickened at their root, and secrete honey from a yellow tissue opposite the ovary (e.g. in *Telephium Imperati*), or a pair of honey-secreting

warts are found at the base of each filament (e.g. in *Alsine mucronata* and *verna*). Sometimes again only the stamens opposite the calyx have swollen bases which secrete honey on the grooved side opposite the ovary (e.g. *Cherleria sedoides*). In the flowers of *Sagina Linnæi* each of the thread-like stamen-filaments opposite the calyx is surrounded at the base by a cup-shaped nectary. Very often the nectaries of adjacent stamens, in the flowers of the above-mentioned plants, fuse together into a ring, the fusion being only just indicated in the Geraniaceæ, but more decidedly in many Caryophyllaceæ (e.g. in *Spergula*), and still more amongst Linaceous and Caryophyllaceous plants (*Linum*, *Gypsophila*, *Dianthus*, *Lychnis*). In the flowers of most Papilionaceæ the stamens form the nectar. Nine stamens are fused into a tube in which the ovary is inclosed. This ovary is at the base



Fig. 247.—Flower of the Snowdrop (*Galanthus nivalis*).

of the flower narrowed into a stalk, while the tube, on the other hand, is somewhat widened. Thus is formed a cavity into which honey is poured from the adjacent part of the staminal tube. The space is covered over by the tenth stamen, which, however, yields no honey. In *Atragene alpina*, belonging to the Ranunculaceæ, the abundant honey so eagerly sought by humble-bees is formed in the deeply-grooved inner side of the stamens (cf. figs. 246<sup>3, 4, 5</sup>).

Very often nectar is secreted by the floral-leaves, both in flowers where they form a perianth and also in those where they may be divided into calyx and corolla (cf. vol. i. p. 641). In the Snowdrop (*Galanthus nivalis*, see fig. 247), the honey is formed in parallel longitudinal grooves on the inner side of the three outspread perianth-leaves; in Lilies, especially those with hanging flowers and curled perianth-leaves, e.g. *Lilium Chalcedonicum* and *Carniolicum* and the well-known Martagon Lily (*Lilium Martagon*), each perianth-leaf is traversed by a channel studded with bands or ramifying swellings, and filled to overflowing with the abundant nectar secreted in it. Several Orchids, especially species of Twayblade (*Listera*), also exhibit such a channel swollen with sweet sap, but only on one of the perianth-leaves, the lip, which is at the same time the resting-place for the honey-seeking insects while they clear out the channel. In the perianth of the Helleborine (*Epipactis*) the lip is deeply grooved, and resembles a boat filled with honey. In *Epipogium* the perianth-leaf corresponding to the lip is arched like a helmet or cap, and covers the abundant honey there produced. In many other Orchids the lower lip of the perianth is produced backwards, and in the expansion (called the *spur* in descriptive Botany) a quantity of honey is usually hidden. The perianth of *Tricyrtes pilosa* (cf. fig. 251<sup>4</sup>) is composed of six leaves, of which the three outer are expanded near their base and secrete abundant nectar. In the flowers of the *Narcissus* (fig. 248), *Gladiolus*, and *Iris*, also in those of *Sisyrinchium* and *Thesium*, the inner side of the tubular perianth is transformed either wholly, or, at any rate, in the lower third into a honey-secreting tissue

without the development of any special expansion. The nectaries are unusually well-developed on the perianth of the American *Uvularia grandiflora*, in the numerous species of *Fritillaria*, and especially in the Crown-Imperial, often cultivated in gardens under the name of *Fritillaria imperialis*. Each of the six perianth-leaves in these plants exhibits on the inner side near the thickened base a circular, sharply-defined depression in which sparkles a large drop of honey.

Honey is seldom secreted by the calyx. The best examples are the coloured, expanded and fleshy calyx of the various species of the genus *Cuphea* and of the Nasturtium (*Tropæolum*). The species of the last-named genus have a calyx from whose upper portion a long spur projects. Honey is secreted in the narrowed lower portion of this spur, and indeed so abundantly that it sometimes reaches to the mouth.

And now we come finally to the nectaries in the region of the corolla. Those developed at the base of the flower as well as on the carpels, stamens, perianth-leaves, and calyx, though strikingly varied, are poor in comparison with the wealth of forms which are shown in the petals. In this book it is impossible to give an exhaustive description of these structures, and it must suffice to group together generally the most striking forms and those best fitted to illustrate the processes hereafter to be described. In the corollas of the Mulleins, especially in those of *Verbascum Blattaria* and *phœniceum*, the secretion of honey takes place on the large, lower petal in the form of numerous drops scattered over the middle of the leaf.

Each drop comes from a stomate, and, therefore, when the flower opens this leaf looks as if it were studded with dew. But this seldom happens. More usually the small drops flow together, and then a large drop appears in some special spot. In the twining Honeysuckles (*Lonicera Caprifolium*, *etrusca*, *grata*, *implexa*, *Periclymenum*, &c.), in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*), in *Allionia* and *Crucianella*, in a species of Winter-green (*Pyrola secunda*), as well as in numerous other plants, honey is secreted in the manner just described in the lowest part of the tubular or bell-shaped corolla. In the Alpine Roses (*Rhododen-*



Fig. 248.—*Narcissus* (*Narcissus Pseudonarcissus*). 1 The complete flower. 2 The flower cut longitudinally.



*dron ferrugineum* and *hirsutum*), as well as in *Monotropa*, the honey-secreting portion of the corolla is thickened and fleshy, and each of the petals, which are fused together, is hollowed into a groove at the base. In the rotate corollas of *Ophelia*, belonging to the Gentian family, each of the petals is provided with a nectar-depression at its base. In the flowers of the non-twining Honeysuckles (*Lonicera alpigena*, *nigra*, *Xylostemum*, &c.) the corolla possesses a honey-forming expansion above the base, and in the flowers of the Calceolarias (*Calceolaria amplexicaulis*, *floribunda*, *Pavonii*, &c.) the nectary is hidden in the end of the up-turned lower petal as if in a shell. The corolla of the Valerian (*Valeriana globulariæfolia*, *montana*, *officinalis*, &c.) manufactures its honey in a small expansion which may be seen on the side of the corolla-tube (cf. fig. 249), and in

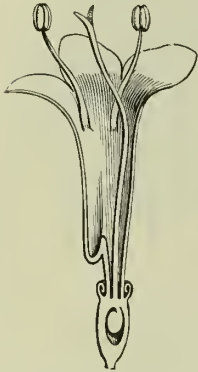


Fig. 249.—Flower of the Wild Valerian (*Valeriana officinalis*), cut through longitudinally.

the flowers of the Butterwort (*Pinguicula*) the corolla is narrowed backwards into a pointed spur (cf. Plate II. opposite p. 143, vol. i.). In the flowers of the Pansy (*Viola*), only one of the five petals has a honey-collecting spur; in those of the Columbine (*Aquilegia*), on the other hand, each of the petals is drawn out into a spur which develops honey in its club-shaped, thickened end. The small white petals of the Sundew (*Drosera*) terminate at their base in a yellow claw whose tissue secretes a little honey. The same thing occurs in the flowers of the Buttercup (*Ranunculus*), only here the honey-producing tissue is sharply defined and appears as the lining of a circular or oval depression, which, in many cases, is uncovered—as, for example, in *Ranunculus alpestris*—but in others is roofed in by a scale, as in *Ranunculus glacialis* (see figs. 246<sup>6, 7, 8</sup>). The flowers of *Hypocoum* have two opposite petals, each divided into three lobes, and at the base of these, under the central lobe, a large pit is developed which is filled with the honey abundantly secreted there (see figs. 251<sup>5</sup> and 251<sup>6</sup>). The nectaries in the flowers of *Swertia*, belonging to the Gentianaceæ, are very remarkable. Two pits surrounded by a strong circular wall are seen some millimetres above the base of the flower on each petal, and a long fringe like a portcullis hangs down from this wall over the pit. The tissue which forms the lining of the pit develops a quantity of honey, and as the grating does not completely cover the pit the honey may be seen shining through it.

We must also consider here those remarkable nectaries interpolated between the floral-leaves and stamens of many Droseraceæ, Berberidaceæ, and Ranunculaceæ, to which the name of “honey-leaves” has recently been given. They display the most peculiar forms, and correspond but slightly to the description commonly given of a leaf. For example, in the Grass of Parnassus (*Parnassia*, fig. 267<sup>5</sup>), belonging to the Droseraceæ, they resemble a hand, on the concave side of which are two honey-secreting depressions, the eleven slender processes which correspond to the fingers terminating in rounded heads. In the flowers of *Epimedium*, belonging to the Berberidaceæ, they are shaped like a slipper. In those of Love-in-a-mist

(*Nigella*), of the Ranunculaceæ, they resemble a covered bowl with a stem, or a hanging lamp (see figs. 250<sup>4</sup>, 5, 6, 7). In the flowers of the Monkshood (*Aconitum*), they take the shape sometimes of a Phrygian cap, sometimes of a cowl, and occasionally of a French horn, and are carried by a long, erect stalk traversed by a channel. In the flowers of the *Isopyrum* as well as in those of *Cimicifuga*, they resemble shovels or spoons, which carry two puzzling knobbed processes at their free ends. The flowers of the Winter Aconite (*Eranthis*), and of the Christmas Rose (*Helleborus*), exhibit nectaries of a trumpet, cup, or tubular form with obliquely-truncated mouth within the large calyx, and those of the Globe-flower (*Trollius*) conceal numerous spatulate nectaries, which are somewhat bent and thickened in the lower third, where they are provided with a honey-secreting pit (see fig. 221<sup>3</sup>, p. 110). In the flowers of the Pasque-flower (*Pulsatilla vernalis* and *vulgaris*), between the large, flat floral-leaves, and the anther-bearing stamens, small club-shaped structures are interpolated in two or three spiral series. These secrete abundant honey which moistens the base of the neighbouring stamens. All these honey-leaves may be regarded either as modifications of petals or of stamens. Those of *Epimedium*, Love-in-a-mist, Monkshood, and *Isopyrum*, remind one more of the former, those of the Globe-flower and Pasque-flower of the latter. The opinion was stated in vol. i. p. 646, that all perianth-leaves might be metamorphosed stamens, consequently it is idle to inquire whether the honey-leaves are to be regarded as petals or as stamens.

From the point of view of the visits of animals these questions as well as others of speculative morphology are unimportant. But, on the other hand, it is of importance to group together into two divisions those nectaries which we have hitherto but cursorily noticed from a morphological aspect. One of these divisions will comprise the nectaries whose sweet fluid is exposed to the daylight, the other those in which the honey is concealed in hidden nooks at the base of the flower.

The exposed honey is accessible to all flower-visiting animals, but can be appropriated with good results only by some of them. The varnish-like coating of honey, for example, which is spread over the cushion of tissue on the ovary of the Spindle-tree, Ivy and Cornel, Saxifrages and Umbelliferous plants cannot be sucked up by butterflies and humble-bees with long probosces. But it is just this honey which is the centre of attraction for beetles, flies, gnats, and other insects with short probosces. On the flowers of the plants named there are actually swarms of beetles of the genera *Anthrenus*, *Dasytes*, *Meligethes*, *Telephorus* and *Trichius*, as well as innumerable flies and gnats which lick up the thin layer of honey with their tongues or their flatly-extended probosces. And the honey which is displayed in the form of large drops in the depths of the lip of the flowers of the Helleborine (*Epipactis*), and in the corolla of the Figwort (*Scrophularia*) is sought for only by insects with short probosces, particularly by wasps, while it is avoided by humble-bees and butterflies.

With the honey hidden in concealed pits, tubes, and channels, exactly the opposite occurs. This is inaccessible to most of the insects with short probosces

but forms the principal food of humming-birds, butterflies, humble-bees, &c. Of course there is again the utmost variety according to the length of the proboscis or bill, and the depth of the hiding-places in which the honey is concealed. The distance of the honey-secreting base from the restricted mouth of the corolla amounts in the flowers of the Heath (*Erica carnea*) to only a few millimetres, while it reaches 16 centimetres in those of the Rubiaceous *Oxyanthus tubiflorus*, which grows in Sierra Leone. In *Angræcum sesquipedale*, a species of Orchid growing in Madagascar and distinguished by the size and splendour of the

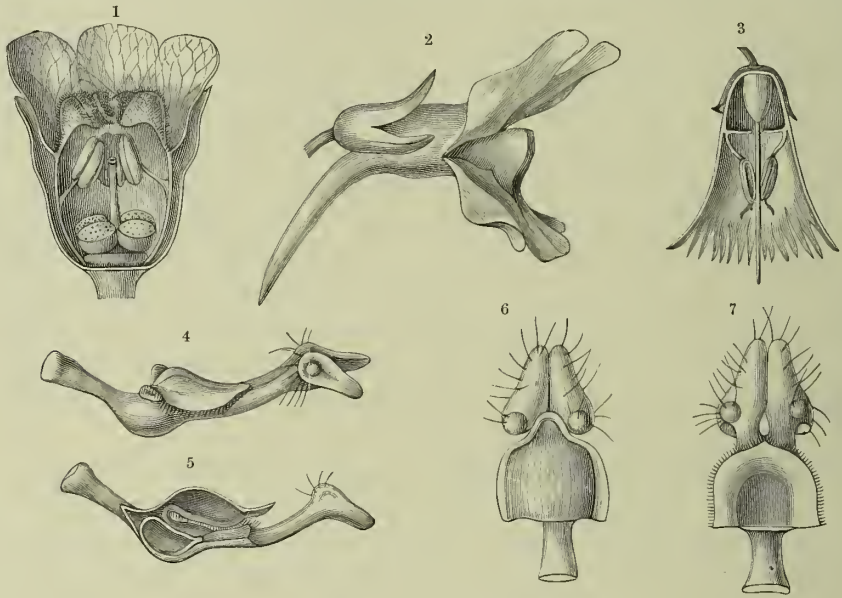


Fig. 250.—Concealment of Honey.

<sup>1</sup> Flower of *Cynoglossum pictum*, the front part of the flower cut away. <sup>2</sup> Flower of *Linaria alpina*. <sup>3</sup> Flower of *Soldanella alpina*, the front part of the flower cut away. <sup>4</sup> A honey-leaf of *Nigella elata*. <sup>5</sup> The same cut through longitudinally. <sup>6</sup> A honey-leaf of *Nigella sativa*, seen from above. <sup>7</sup> The same; the roof covering the nectar-pit cut away. All the figures somewhat enlarged.

inflorescence, the perianth possesses a hollow spur 30 centimetres long which is filled with honey at its base.

There are two kinds of contrivances for hiding the honey in pits, tubes, and channels. In the one the entrance to the hiding-place is narrowed by all kinds of inflations, cushions, bands, and flaps at the mouth of the flower-tube (see fig. 250 <sup>1</sup> of the flower of *Cynoglossum*). In the other the nectary is completely closed over by a roof or door, or by two lips, so that those animals which desire the honey stowed away in the cavity are compelled either to raise the roof, to open the door, or to press down one of the lips. As examples of the latter kind of closing may be instanced the flowers of *Corydalis*, of the Fumitory (*Fumaria*), of the Snapdragon (*Antirrhinum*), and of the Toad-flax (*Linaria*; see fig. 250 <sup>2</sup>), whilst in some Soldanellas (*Soldanella*; see fig. 250 <sup>3</sup>), and in the genus *Aechmea*, belonging to the Bromeliaceæ, the closure is effected by special scales, like folding doors, introduced into the corolla-tube.



Sometimes the stamens are so fashioned and disposed as to form an overarching roof or dome above the honey-secreting base of the flower, *e.g.* in numerous Solanaceæ, Primulaceæ, Boraginaceæ, and Campanulaceæ (*Nicandra*, *Cyclamen*, *Borago*, *Campanula*, *Phyteuma*); very beautifully also in the Willow-herb (*Epilobium angustifolium*), in *Gladiolus*, and in the small-flowered Cinquefoil (*Potentilla micrantha*) pictured in fig. 246<sup>1</sup>; finally in the Mammillarias, belonging to the Cactaceæ (see fig. 246<sup>2</sup>).

The hiding of the nectaries by a massing together of the stamens is effected in

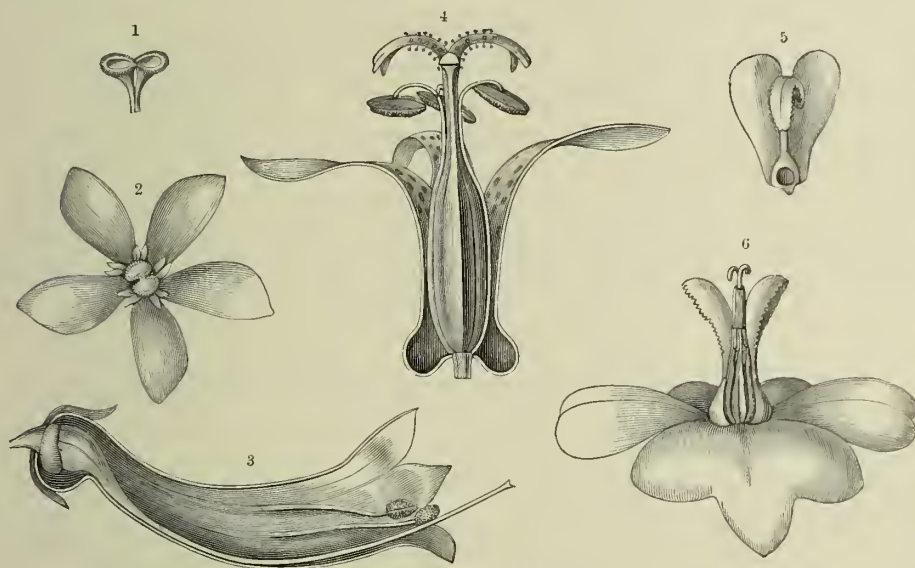


Fig. 251.—Concealment of Honey.

<sup>1</sup> Stigma of *Gentiana Bavarica* which closes the corolla-tube, removed from the flower. <sup>2</sup> Flower of the same plant seen from above. <sup>3</sup> Flower of *Phygadeuon capensis*; the front half cut away. <sup>4</sup> Flower of *Tricyrtes pilosa*, the anterior part cut away. <sup>5</sup> One of the two inner petals of *Hypecoum grandiflorum* seen from the side adjacent to the ovary. <sup>6</sup> Flower of *Hypecoum grandiflorum* showing the two inner petals standing close to the ovary.

a very strange manner in some white-flowered Crow-foots, *e.g.* in *Ranunculus glacialis*. In these plants the honey is secreted in small pits on the upper side of the petals close above the yellow, thickened claw (see fig. 246<sup>6, 7, 8</sup>). In front of this pit is a scale which rises from the plane of the petal at an angle of 40°–50°. On and near this scale lie the numerous stamens arranged in several whorls radiating out from the centre of the flower. A small nectar-cavity is thus formed at the base of each petal to which only those insects strong enough to press up the overhanging stamens and the scale can gain entrance. In the flowers of the *Atragene alpina* the stamens are hollowed into a groove in which a quantity of honey is secreted (see fig. 246<sup>4</sup>). But as in each flower there are many whorls of stamens—those of the outer whorls always covering and being attached to the backs of the inner ones (see fig. 246<sup>3</sup>), and as all the stamens are held together outside by a whorl of erect, stiff, spoon-shaped leaves (see fig. 246<sup>5</sup>)—all these channels form, as it were, many small, closed, nectar-cavities only to be opened by powerful insects.

The flowers of the *Phygelius capensis* (illustrated in fig. 251<sup>3</sup>) show at the base of the tubular corolla a small expansion filled with honey which is converted into a closed cavity by the ovary bending down in front of it and pressing itself closely to the wall of the corolla-tube. In the flowers of *Tricyrtes pilosa* (see fig. 251<sup>4</sup>), whose three outer perianth-leaves secrete honey in the expansion at the base of the flower, the three-sided ovary is wedged in like a prop between the perianth-leaves, and three closed nectaries are thus formed out of the expansion. A similar appearance is also observed in the flowers of *Hypecoum procumbens*. Here the honey is secreted in a pit close above the claw of the two inner petals (see fig. 251<sup>5</sup>). Just as in *Ranunculus glacialis*, so here, this pit is covered by a peculiar scale which is fitted to receive the pollen at a certain stage of development, as will be afterwards described. This scale is erect and parallel to the ovary, its base being in contact with it (*cf.* fig. 251<sup>6</sup>). In this way the pit or nectary is completely closed in.

It may be remarked finally that in many cases the stigma may act as a covering to excavated, honey-containing flowers. This is so, for example, in the Gentians of the group *Cyclostigma*, the flower and stigma of one species of which (*Gentiana Bavarica*) are illustrated in figs. 251<sup>1</sup> and 251<sup>2</sup>.

#### THE COLOURS OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

If we wish that certain distant objects should be plainly seen, it is usual, as is well known, to assist the eye by contrasts of colour. We place signals on the railways with a red band on a white background, put gold letters on black sign-boards, and paint a black circle and a black spot on the white disc towards which we point the gun. The same colour-contrasts occur in plants whose flowers are the aim of flying animals.

Since flowers in most cases open above green foliage-leaves, it is evident why in the floral region those colours are most often met with as allurements which contrast well with green. Of those plants of the Baltic flora whose flowers are displayed against a background of green, 33 per cent are white, 28 per cent yellow, 20 per cent red, 9 per cent blue, 8 per cent violet, and 2 per cent brown. Looked at from a distance white, yellow, and red stand out best from the green of the foliage, blue and violet only a little, and brown scarcely at all.

Usually it is the petals whose colour standing out from the surroundings makes the flowers conspicuous from a distance. That side which is presented towards the flying insects displays the colour most brightly. When the corollas or perianths are pitcher-shaped or bell-shaped, nodding or pendulous, so that the animals on approaching do not see into the inside of the flower, the outside is coloured the more brilliantly. But if, on the other hand, the flower is star-shaped or disc-like, with its face turned to the sky, and to the swarming insects, then the inner side shows the brighter colours. There are even some flowers whose petals are

coloured yellow, white, or red on the inside only, while the outer side is green. Those, for example, of *Gagea* are yellow on the inside only whilst the outside is green. When these flowers are closed they do not strike the eye; only when opened in the sunlight does the yellow star show up from the background. The same thing may be said of the flowers of the Star of Bethlehem (*Ornithogalum*), of the Lesser Celandine (*Ranunculus Ficaria*), of the Pimpernel (*Anagallis*), of the Venus's Looking-glass (*Specularia*) and of many other plants.

In some instances where the petals have been transformed into nectaries, or have assumed some other function, which would not easily allow of their developing brightly-coloured surfaces, the duty of alluring the animals is performed by the sepals. These are then not green, but are coloured white, yellow, red, blue, violet, or brown, as, for instance, those of the Christmas Rose and of the white Wood Anemone (*Helleborus niger*, *Anemone nemorosa*), of the Globe-flower and Winter Aconite (*Trollius*, *Eranthis*), of the Atragene and of the Monkshood (*Atragene alpina*, *Aconitum Napellus*), of the Pasque-flower and of the Marsh Cinquefoil (*Pulsatilla pratensis*, *Comarum palustre*). And of course the features noted above in the case of the petals is repeated in these flowers—the outer side of the calyx is brightly coloured in the hanging bells of the Marsh Cinquefoil, but the inner side in the star-shaped, open flowers of the Pasque-flower.

Nor do the stamens, in comparison with the corolla, calyx, or perianth, frequently serve as attractive organs to animals in virtue of peculiar colouring. In Northern and Central Europe we notice the Willows—destitute of perianth-leaves—rendered conspicuous from afar by their numerous, crowded stamens with red or yellow anthers. In other cases the flowers are conspicuous in virtue of their brightly-coloured stamen-filaments—white, purple, red, or yellow—as in certain Ranunculaceæ, e.g. *Actæa*, *Cimicifuga*, and *Thalictrum*, still more in the Acacias of Australia, and in the genera *Callistemon* and *Metrosideros* belonging to the Myrtaceæ, in the Japanese *Bocconia*, as well as in several species of *Æsculus* (e.g. *Æ. macrostachya*). The flower-spikes of the North American *Pachysandra*, which trail along the ground, yet stand out from the dark environment because the filaments are dazzling white. In several Asiatic Steppe-plants, viz. in species of *Halimocnemis* (see figs. 252<sup>10</sup> and 252<sup>11</sup>), a bladder-like appendage rises above each anther, and is coloured sulphur-yellow, violet, bright or dark red, and thus stands out brilliantly from the gray-green surroundings and might easily be mistaken at first sight for a petal.

It often happens that the bracts which subtend and enfold the flowers rather than the flowers themselves attract attention by the contrast of their colours with the surrounding green. Numerous examples are furnished by the Cornel (e.g. *Cornus florida* and *Suecica*; see fig. 252<sup>12</sup>), the Myrtaceæ (*Genetyllis tulipifera*), the Umbelliferæ (*Astrantia*, *Bupleurum*, *Smyrniun*, *Eryngium alpinum*), the Labiateæ (*Nepeta reticulata*, *Salvia splendens*), Compositæ (*Cirsium spinosissimum*, *Gnaphalium Leontopodium*, *Xeranthemum annuum*, *Carlina acaulis*; see p. 117), the Spurges (*Euphorbia polychroma*, *splendens*, *variegata*), the Aroids



(*Richardia æthiopica*, *Anthurium Scherzerianum*), and the Bromeliaceæ (*Nidularia*, *Lamprococcus*, *Pitcairnia*). In some Proteaceæ, e.g. *Protea globosa*, the uppermost foliage-leaves are grouped into a large outer envelope which surrounds the spherical golden-yellow inflorescence, and these crowded leaves are coloured



Fig 252.—Colour-contrasts in Flowers.

- <sup>1</sup> Umbellate raceme of *Lobularia nummularifolia* with flowers and young fruits. <sup>2</sup> A single young flower of the same plant. <sup>3</sup> A young fruit of the same plant with two of the enlarged white petals attached to it. <sup>4</sup> Flower spike of *Lavandula Stoechas* ending in a crest of empty blue bracts. <sup>5</sup> Umbellate raceme of *Alyssum cuneatum* with young flat open flowers in the centre and old closed flowers at the circumference. <sup>6</sup> Petal of a young flatly-opened flower of the same plant. <sup>7</sup> Petal of an old closed flower of the same plant. <sup>8</sup> Raceme of *Muscari comosum*; the upper long-stalked flowers crowded into a head are sterile. <sup>9</sup> Inflorescence of *Trifolium badium*; the upper young flowers are light yellow, the old lower drooping flowers are dark brown. <sup>10</sup> A branch from the inflorescence of *Halimocnemis mollissima*; the erect bladder-like appendages of the anthers protrude from the insignificant perianth and look like petals. <sup>11</sup> A single stamen of *Halimocnemis mollissima*; the connective rises above the anther in the form of a bladder-shaped appendage. <sup>12</sup> Inflorescence of *Cornus florida* surrounded by four large white bracts. <sup>13</sup> Cornflower (*Centaurea Cyanus*); the small flowers of the disc are surrounded by large funnel-shaped sterile flowers. <sup>14</sup> Raceme of *Kerneria saxatilis*; the ovaries in the centre of the old flowers are darkly coloured and surrounded by the enlarged petals. <sup>15</sup> Inflorescence of the umbelliferous *Orlaya grandiflora*; the peripheral flowers radiate outwards. <sup>16</sup> A single radiating flower of the same plant. <sup>17</sup> Umbellate raceme of the Candytuft (*Iberis amara*); the outwardly-directed petals of the peripheral flowers are twice as large as those which are turned towards the centre of the inflorescence. <sup>2</sup>, <sup>3</sup>, <sup>11</sup> are somewhat magnified; the others natural size.

blue in contrast to the lower, scantier foliage, which has a grass-green colour, in order that the inflorescence should stand out the better. Even the stalks of flowers and inflorescences when brilliantly coloured may be seen from a distance and so



VICTORIA REGIA IN THE RIVER AMAZON.





furnish a means of allurement, as is the case in *Eryngium amethystinum*, *creticum*, &c., as well as other plants.

When a coloured object is less than a certain size not even the most vivid red, the brightest yellow, or most dazzling white will render it visible at a distance. If the parts of the flower or the envelopes whose function is to attract flying animals from a distance are to be serviceable as signs, they must occupy a considerable space, a necessity provided for in various ways, one of which is the large size of the individual flower. But it would be an error to suppose that this method, from its apparent simplicity, is the most frequent; in point of fact it seldom occurs. Scarcely one in a thousand of the flowers of Phanerogams exceeds 10 centimetres in diameter, and most of these are found only in tropical countries. A species of *Rafflesia*, which has the largest flowers in the world, is illustrated in vol. i. p. 203. The *Rafflesia Schadenbergiana*, which flourishes in the Island of Mindanao in the Philippines at a height of 800 metres above the sea, parasitic on the roots of *Cissus* plants, develops flowers weighing about 11 kilograms a-piece, with a diameter of about 80 centimetres. To be mentioned with these *Rafflesias*, in respect of extreme diameter, are the flowers of the rare Peruvian orchid, *Paphiopedilum* (*Cypripedium*) *caudatum*, whose ribbon-like lateral petals attain a length of 70 cm. These tailed lateral petals hang down moustache-like right and left of the flower, and though when the flower first expands they are only some 10 cm. long, they continue growing for about ten days, in which time they usually attain their full length. From the second to the seventh day they have been observed to increase in length as much as 5 cm. each day. Very large also are the balloon-like flowers of several tropical American *Aristolochias*, of which it is stated that children use them in play as caps and pull them down over their heads. Thus the flowers of the Guatemalan *Aristolochia gigas*, var. *Sturtevantii* (cultivated in the Botanic Gardens at Kew) are about 45 cm. wide, 55 cm. long, with a tail exceeding a metre in length; their colour is creamy yellow and deep maroon purple. But of course the amount of substance composing these tailed and inflated flowers is as nothing compared with that which goes to make a huge *Rafflesia*-flower. The flowers of *Magnolia Campbellii* belonging to Sikkim (Himalaya) display almost as great a diameter as those of these tropical creepers. When the erect red flowers of this tree open in the sunshine they show a width of 26 cm., a size never attained by any other tree-flower. One of the Lotus plants, viz. *Nelumbo speciosum*, as well as the Australian *Nymphaea gigantea*, produces flowers with a diameter of 25 cm.; the *Lilium auratum*, recently much planted in European gardens, flowers of 24 cm. Many Cactuses exhibit flowers with a diameter of 20–22 cm., viz., *Echinopsis cristata*, *Cereus grandiflorus*, the Queen of the Night (*Cereus nycticalus*), shown in Plate VII. (vol. i. p. 641), the South American *Datura Knightii*, *Nymphaea Devonensis*, and the celebrated *Victoria regia*, represented in the accompanying Plate XI., “*Victoria regia* in the River Amazon”. *Nelumbo luteum*, *Amaryllis solandriiflora*, and the Opium Poppy (*Papaver somniferum*) have flowers of 16–18 cm. diameter, *Amaryllis aulica* and *equestris*, *Datura ceratocaula* and *Pæonia*

*Moutan* of 13–15 cm., several Mexican Cactuses (e.g. *Echinocactus oxygonus* and *Tetani*) and the Gourd (*Cucurbita Pepo*) flowers of 10–12 cm. diameter.

Another method by which flowers are rendered conspicuous to the naked eye is the massing together in bunches, spikes, racemes, umbels, and capitula. A single flower of the Elder (*Sambucus nigra*), with a diameter of only 5–6 mm., would be scarcely visible on its dark background at a distance of 10 paces, while a thousand or fifteen hundred of such flowers arranged in a flat nosegay of 16–18 cm. diameter show up quite plainly at the same distance from the dark-green foliage. Even the flowers of the American weed, *Galinsoga parviflora*, recently established in Europe, which are amongst the smallest in the world, having only a length of 1 mm. and diameter of 0.3 mm., become so conspicuous when crowded together in great numbers on a flat disc that they may be easily distinguished by the eye at a distance of 15 paces. The flowers of about 10,000 different Composites, 1300 Umbelliferæ, and innumerable Valerians, Pinks, Stitchworts, Spiræas, Papilionaceæ, and Labiatae are only visible at a distance because crowded together. If isolated their minuteness would prevent them from being noticed.

Very often it is only a part of the flowers which, when collected into umbels, racemes, and capitula, make the whole conspicuous. In species of *Iberis* belonging to the Cruciferæ (e.g. *Iberis amara*, *gibraltarica*, *umbellata*; cf. fig. 252<sup>17</sup>), in most Scabiouses (e.g. *Scabiosa Columbaria*, *cretica*, *graminifolia*), and in not a few Umbelliferæ (*Daucus*, *Heracleum*, *Orlaya*; cf. figs. 252<sup>15</sup> and 252<sup>16</sup>), the flowers growing at the circumference of the umbel or capitulum show an enlargement on one side; i.e. those petals which are turned away from the centre of the inflorescence are considerably increased and look like short rays proceeding from the periphery. Some Cruciferæ of the genera *Alyssum*, *Dentaria*, and *Sisymbrium* are also remarkable instances. It cannot be said of these that the flowers standing at the circumference of the umbellate group are really enlarged on one side, yet they have the same appearance as the radiating flowers. This is accounted for by the fact that the petals do not fall off after the deposition of pollen on the stigmas, but remain behind, fold together like the leaves of a book, and, what is still more remarkable, after a little while grow together. When the flowers of *Alyssum montanum*, *Wulfenianum* and *cuneatum* (cf. fig. 252<sup>5</sup>) reach the highest point of their development, when pollen is formed by their anthers, and honey for insects stored in the flower base, the yellow petals have a length of 3–4 mm.; but when once the anthers have given up their pollen and the flower base is cleared of its honey, when the stigma has dried up and the ovary has already grown into a small fruit, then the petals attain a length of 6–7 mm. (cf. figs. 252<sup>6</sup> and 252<sup>7</sup>). Thus, while the flowers which have just reached maturity and stand in the centre of the group are small and insignificant, those at the circumference display enlarged petals radiating outwards, thus rendering the whole inflorescence conspicuous. In other words, the older flowers are actually occupied in the allurement of insects for the advantage of the younger ones.

The difference between the peripheral and central flowers of one and the

same head does not always consist only in the enlargement of one side, but in many plants in the actual development of different forms of flower. In these the flowers of the centre stand erect and are tubular, while those of the periphery radiate outwards, are larger, coloured much more brilliantly, and are shaped either as short broad plates as in the Milfoil (*Achillea*), or like long narrow tongues as in *Arnica montana*. In the Cornflower (*Centaurea Cyanus*, cf. fig. 252<sup>13</sup>) and in allied species the peripheral flowers assume the form of funnels with split edges. One seeks in vain for anthers and stigmas inside these flowers; they have become unfruitful and sterile, and in this way a complete division of function has taken place in the two kinds of flowers of the Cornflower capitulum. Here it is only the flowers of the centre which are provided with stamens and pistils, and which conceal honey at the base of their small tubes; these alone are fertile. On the other hand, they are insignificant in appearance, and at a little distance would not be noticed. Thus the sterile, funnel-shaped flowers, visible from a distance on account of their beautiful azure blue, surround their fruitful neighbours, and perform the task of attracting the insects to them. This remarkable division of labour in flowers of one and the same capitulum seen in Cornflowers may be also noticed in many cymose inflorescences—as, for example, in the Guelder-rose (*Viburnum Opulus*) and in Hortensias (*Hydrangæa Japonica*, *quercifolia*, &c.; cf. fig. 222<sup>8</sup>). Of course only in the wild specimens, for the Guelder-rose grown in gardens, as well as those plants which horticulturists call Hortensias, have inflorescences consisting entirely of sterile flowers from which no fruit can be produced.

While in the last-mentioned plants the sterile flowers which attract insects are found at the circumference of the capitulum or umbel, one meets with a bunch of sterile flowers at the top of the racemose inflorescence in many species of *Muscari*, allied to the Hyacinths (e.g. *Muscari comosum* and *tenuifolium*; cf. fig. 252<sup>8</sup>). These are very remarkable on account of their bright colour, and obviously perform the same function on behalf of the less conspicuous fruitful flowers below as do the sterile flowers in the capitulum of the Cornflower.

When the bracts enveloping the flower heads assume the function of alluring insects, and are consequently coloured white, yellow, red or blue, each of these structures singly is usually of such a small size that it could not be seen even at a very little distance; but their aggregate effect is such that the whole inflorescence is conspicuous from afar. The dry scales surrounding the flower-heads are coloured snow-white, golden-yellow, or rose-red in the species of *Helichrysum* known as Immortelles—for example, in the sacred flower which the Greek pilgrims bring with them from Mount Athos (*Helichrysum virgineum*), in the beautiful *Helichrysum frigidum* of the Corsican uplands, in the yellow-headed *Helichrysum arenarium* growing on the sandy heaths of the Rhine valley, and in the numerous species spread over the rocky heights in the Cape. It is evident that the effect of the scaly, coloured envelopes is materially increased when the flower-heads they surround are massed together in numbers forming dense tufts. It thus happens



that inflorescences whose individual parts only measure a few millimetres may be plainly seen at a distance of many hundred paces. Fig. 253 is an illustration taken from nature of the Haastias (*Haastia pulvinaris* and *Sinclairii*), composites which grow in New Zealand on mountains of 1200 to 2000 metres in height, and are a good example of the above. The innumerable flower-heads of this plant are crowded together into hemispherical masses which reach a height of half a metre with the diameter of a metre. Both the scaly envelopes and the flowers are coloured white, and since these Haastias grow on rocky heights upon a background



Fig. 253.—Two New Zealand Haastias (*Haastia pulvinaris* and *Sinclairii*, the latter species in front) called “vegetable sheep” by the English colonists in New Zealand.

of dark earth and stone they stand out conspicuously from their surroundings. The colonists name these plants “vegetable sheep”, often mistaking them, so it is said, for fugitives from their flocks, and take long journeys in order to bring them back, only discovering the true state of the case to their great annoyance when close at hand.

The bracts of many species of Lavender and Sage (*Lavandula pedunculata*, *Stæchas*, *Salvia viridis*, &c.), growing in the floral region of the Mediterranean, become sources of allurements in a very strange manner. Those which grow beneath the bunches of flowers on the lower half of the spike are insignificant, but at the top, where the flowers are not developed, the bracts are enlarged, brilliantly coloured, and crowded into tufts, resembling the white or red flowers used as

trophies by builders to celebrate the completion of a certain stage of their work (cf. fig. 252<sup>4</sup>).

The plants which have hitherto been selected to illustrate the significance of colour in flowers, whether in the blossoms themselves or in their bracts, exhibit only one tone of colour in contrast with the foliage green; that is to say, the entire flower, the whole inflorescence, or the complete group of bracts appears from a little distance as simply white, yellow, red, violet, or blue, and stands out conspicuously from the environment on account of one of these colours. It often happens, however, that the colour-contrast is obtained by the development of several colours in the flowers. In the blossoms of many Willow-herbs (e.g. *Epilobium hirsutum* and *montanum*), the white cross formed by the stigmas appears on a red field; in the Herb Paris (*Paris quadrifolia*) the bright yellow anthers encircle the large, dark-violet ovaries. In the centre of the flowers of the Borage (*Borago officinalis*) a black cone of anthers rises from a blue star, and a yellow cone of anthers on a violet star in the Bitter-sweet (*Solanum Dulcamara*) and in the Potato. In the flowers of the Pheasant's-eye (*Adonis flammea*, *æstivalis*, *autumnalis*), the numerous black anthers form a dark centre on a red ground, and an orange centre on a blue ground in the Jacob's Ladder (*Polemonium cœruleum*), whilst in the flowers of the Hepatica (*Anemone Hepatica*) a white centre is seen on a blue ground, and in the flowers of many Mulleins (*Verbascum austriacum*, *nigrum*) occur stamens with violet hairs which contrast with the light yellow corolla and orange anthers. The dark violet petals of *Saxifraga biflora* surround a centre of golden-yellow, and in the Ice-plant (*Mesembryanthemum crystallinum*), so common at the Cape, the yellow centre formed by the crowded anthers is surrounded by a large number of narrow, radiating, red petals.



Fig. 254.—Colour-contrast in the flowers of the Bean (*Vicia Faba*). The wings (alæ) of the white papilionaceous corolla are ornamented with large black eye-spots.



In all these instances the stigmas and stamens stand out from the petals, but it may happen that the floral-leaves themselves are thus conspicuous, as, for example, in the flowers of *Victoria regia*, whose outer petals are white, and the inner crimson (see Plate XI. opposite p. 185). In Papilionaceous flowers it is often observed that the upwardly curved petal called the standard is coloured differently from the keel and the wings. The Vetches and Peas (*Vicia picta*, *Lathyrus odoratus*, *Baptisia australis*) may be quoted as examples. Those Papilionaceous flowers are most remarkable in which the two lateral wings are dark violet or



Fig. 255.—Narcissus (*Narcissus poeticus*); the Corona in the centre of the flower is fringed with a cinnabar-red border (black in the figure).

almost black, and look like two dark eyes below the yellow standard (e.g. in *Vicia Barbazetæ*, *Melanops*, and *Faba*; see fig. 254). In thousands of flowers the petals are marked with spots, speckles, stripes, bands, and borders, the contrasting colours being set next one another. The white perianth-leaves of the Snowflake (*Leucojum vernum*; cf. fig. 244) have a green spot near the apex; the scarlet-red standard of the butterfly-corolla of *Clianthus Dampieri* carries a dark-violet eye-spot in the centre; the orange tongue-shaped flowers of *Gorteria ringens* have a black spot at the base, in which are scattered white stripes and dots; the delicate perianths of *Sisyrinchium anceps* are blue or violet above, but yellow or orange below. The white coronas of the Narcissus (*Narcissus poeticus*; cf. fig. 255) are surrounded by a cinnabar-red border; and in the blue flowers of the Forget-me-not (*Myosotis*), the mouth of the short tube

has an irregular yellow ring round it. Those plants which have been called “tricolor” on account of the various tints of their flowers, e.g. the three-coloured Bindweed (*Convolvulus tricolor*), the Pansy (*Viola tricolor*), and the three-coloured Vetch (*Vicia tricolor*), may also be quoted as examples.

Sometimes the spots, points, and stripes standing up from the ground-colour of the flowers perform the double function of showing the entrance to the honey easiest for the approaching insects, and at the same time most advantageous to the plant itself. Of this we shall speak more particularly later on. But it would be too much to say that all spots are to be regarded as signals or to call them “honey-indicators” or “path-finders”. They are found often enough in flowers from which honey is altogether absent, as, for example, in those of *Hibiscus Trionum*, and of the opium and common red Poppies (*Papaver somniferum* and *Rhæas*), where their only use can be to show up the flowers. It should be noted here that



flowers with finely-marked petals are ardently sought for, indeed, almost exclusively, by flies. Many Orchids and Labiate flowers, but especially many Saxifrages (*Saxifraga Aizoon*, *aizoides*, *bryoides*, *rotundifolia*, *stellaris*, *sarmentosa*, &c.), are very instructive examples. We cannot, indeed, explain what connection there is between the visits of flies and the yellow, red, or violet dots which in some species sometimes change their colour during the period of flowering. But it is certain that the minute red and yellow spots on the petals of these Saxifrages do not make the flowers more visible or conspicuous to the human eye.

A brilliant contrast is caused by the difference in the colours of the corolla and the adjacent outspread bracts and sepals. The flower of *Acanthus*, whose upper sepal is coloured violet, while the petals below it are white, deserves special notice in this connection. Also those of *Clerodendron sanguineum* with white sepals and blood-red petals, as well as the inflorescence of many species of the Cow-wheat (*Melampyrum arvense*, *grandiflorum*, *nemorosum*), whose blossoms are yellow and the bracts blue, violet, or red. Lastly, we may mention *Sideritis montana* and *Romana*, whose small, brown petals project like dark points from the yellow bracts.

In the capitula of Composites whose flowers are crowded closely together, the florets of the ray and of the disc usually display different colours. As examples of this common form of colour-contrast may be mentioned the Ox-eye Daisy (*Leucanthemum vulgare*), whose yellow disc-flowers are surrounded by white ray-flowers; *Pyrethrum carneum*, with yellow disc-flowers and red ray-flowers; Rudbeckias and Zinnias (*Rudbeckia laciniata*, *fulgens*, *Zinnia hybrida*, &c.), whose dark-brown disc-flowers are surrounded by yellow ray-flowers, and almost all the numerous series of Asters with yellow disc-flowers and blue ray-florets.

Contrast of colour is also frequently produced by the corollas changing their colour at various stages of development. In the bud they are red, after opening they become violet, and then when they wither they become blue or malachite green. When such flowers are crowded together a very effective colour-contrast may result. Especially remarkable in this respect are the Bitter Vetches (*Orobus vernus* and *Venetus*), and several Boragineous plants belonging to widely different genera (e.g. *Pulmonaria officinalis*, *Mertensia Sibirica*, *Symphytum Tauricum*), and also some Willows (e.g. *Salix purpurea*, *repens*, *Myrsinites*), in which latter the crowded anthers appear at first purple, red, then yellow, and finally black. The tubular flowers of the flat disc-shaped head of *Telekia* (*Telekia speciosa*) are yellow at first, but later become brown, and since the flowers open successively from the circumference towards the centre of the head, when the blossom is at its height the yellow centre is surrounded by a dark-brown ring. In many species of Clover (*Trifolium*), the faded corollas do not fall off at the end of the flowering period, but wither and dry up, and envelope the small fruit like a mantle. The stalks of the flowers grouped into umbellate heads then bend downwards and arrange themselves into a wreath surrounding the upper, younger flowers which stand erect and are, of course, of a different colour. Thus in the Bastard Clover (*Trifolium hybridum*), the young, erect, densely-crowded, white flowers are

surrounded below by a garland of older, rose-red flowers; and in *Trifolium spadiceum*, the light-yellow centre formed by the young flowers is surrounded by a zone of chestnut-brown older flowers whereby a very remarkable colour-contrast is brought about (cf. fig. 252<sup>9</sup>).

The contrasts met with in the umbel-like racemes of the small-flowered Cruciferae are also extremely varied. These are partly produced by changes of colour during the opening and fading of the flowers, partly by the increase which the petals undergo very noticeably after pollination. In a group of these Cruciferae of which the Whitlow-Grass, the round-fruited Penny Cress, and the Egyptian Lobularia (*Draba verna*, *Thlaspi rotundatum*, *Lobularia nummulariaefolia* (cf. figs. 252<sup>1, 2, 3</sup>) may serve as types, the originally very tiny white leaves of the corolla increase to twice their size, and adhere to the broad side of the ovary, which has meanwhile become much enlarged, and brown or violet in colour. The ovaries, to which the snow-white petals adhere, grow into young fruits, and then form a wreath, just as in the species of Clover described above, around the younger white flowers, as well as the central green buds. The consequence is that the whole inflorescence is rendered conspicuous, although the leaves of the corolla when it opens are small and insignificant.

In a second group of the Cruciferae, of which *Thlaspi alliaceum* and *Thlaspi arvense* may be chosen as examples, the ovaries as they mature into fruits are only slightly discoloured, but the green of the sepals changes in the older flowers into yellow. Thus in each corymb white, yellow, and green appear side by side in a varied play of colour. A third group, of which *Alyssum calycinum*, *Draba aizoides* and *Arabis cœrulea*, may serve as types, is rendered conspicuous by the bleaching of the sepals and petals after flowering. The petals of *Draba aizoides* and *Alyssum calycinum*, which, while blossoming, were golden yellow, become whitish and adhere to the young green fruits. The petals of *Arabis cœrulea* are blue at the commencement of flowering, but fade later on and lie flat on the young fruits, which have meanwhile assumed a violet tint. In these three groups of Crucifers the broad side of the maturing ovary serves as a foil to the pale floral-leaves, which increase in size after fading, and thus a piebald effect is given to the whole inflorescence. In a fourth group, of which the Wild Cress (*Ethionema*) is an example, the young fruits are completely enveloped by the enlarging floral-leaves, and are therefore without significance as regards colour. The contrast is here obtained in the following peculiar manner: The young flowers are supported side by side on short, erect pedicels at the top of a common stem, and their small, expanded petals are all turned with their upper side towards the observer. After fading, the pedicels lengthen, bend sideways, and project horizontally from the common stalk of the whole inflorescence. The petals still grow in length and breadth, and place themselves together like the leaves of a book, so that the side which formerly was the lower one is now turned to the spectator. But, since the upper and under sides of the petals are differently coloured, the young flowers crowded in the centre of the corymb exhibit a different colour from the old ones of

the circumference. This phenomenon is most beautifully shown in species of this genus which grow in the Taurus (*Æthionema grandiflorum* and *diastrophis*) where the white centre of the corymb is surrounded by an ornamental red wreath of older, folded flowers. The species of the genus Bitter Cress (*Cardamine*), which, together with many other Cruciferae, form a fifth group, agree with the species of Wild Cress just described in regard to the enlargement and folding together of the petals, but in them the contrast is not brought about by the juxtaposition of the colours on the upper and under sides of the petals, but by a change of colour in the sepals. The sepals, originally green, become coloured yellow in the older, horizontally-placed flowers, but the colour of the petals remains unaltered, white or violet. Finally, in the flowers of a sixth group, of which *Kernera saxatilis* (fig. 252<sup>14</sup>) may serve as an example, the petals of the older flowers do not fold together and do not adhere to the ovary, but retain the position which they had at the beginning of flowering, *i.e.* they always present the upper side to the beholder. But as the flowers get older the ovary swells enormously and becomes coloured a dark purple brown; it pushes itself between the petals, and these (which have increased considerably) now form a white inclosure to the purple fruit. Thus the old flowers at the circumference of the corymb obtain a spotted, conspicuous appearance.

We have now to speak of the colour contrast which comes into play between different kinds of plants growing in the same district, the flowers of which unfold simultaneously. In a meadow studded with thousands of the blue flowers of the *Campanula*, the orange-coloured stars of *Arnica montana* rising up between them show up much more plainly than if these Bell-flowers were not present. The same may be said of the Bell-flowers whose blue colour is materially heightened by the presence of the orange-coloured stars of the Arnica. It might almost be said that the growth of plants side by side with contrasting colours so frequently observed is arranged in the way here indicated, and the change of colour in the flowers of one and the same species in different regions can also be explained by the fact that contrast of colour is so advantageous to the plants in question. Let us suppose that on a meadow where in summer a plant with red flowers—perhaps a Pink—grows in great quantity, a blue Bell-flower has established itself. Some members of it may bear white flowers, as often happens in this plant. Without doubt these white Bell-flowers show up better than the blue from the red Pinks, and therefore have more chance of being visited by insects and of forming fruit and seeds. In course of time the white Bell-flowers will constitute the overwhelming majority, and the meadow will be studded for the most part with white Bell-flower blossoms growing between the Pinks with their red flowers. If the same Bell-flower had established itself in a field in which orange-yellow flowers grew in great numbers, the blue and not the white-flowered plants would have been visited by insects, since they would be the more conspicuous; thus they would multiply and ultimately prevail.

In the neighbourhood of the Brenner *Campanula Trachelium* bears white



flowers, but blue flowers in the valleys of the Eastern Limestone Alps. The long-spurred Violet (*Viola calcarata*) displays a blue corolla on the meadows of the Western Central Alps, and a yellow corolla in the Eastern Alps of Krain. *Astragalus vesicarius* has yellow blossoms in the Tyrolese Vintschgau, violet on the Limestone Mountains of Hungary. *Melittis Melissophyllum*, in the Southern Tyrol, has white flowers only; whilst in Lower Austria and Hungary it has purplish-white flowers. The Alpine Poppy (*Papaver alpinum*) occurs on the débris-slopes of the Lower Austrian and Styrian Limestone Alps with white flowers, in those of the South-Eastern Limestone Alps, in Krain, with deep yellow flowers. *Anacamptis pyramidalis*, on the north side of the Alps, is only seen with deep carmine-red flowers; in the Dalmatian Islands and in Italy it exhibits pale flesh-coloured blossoms. *Anemone alpina*, on the Central Tyrolese Alps, bears chiefly sulphur-yellow flowers; in the Eastern Limestone Alps its flowers are always white. The crested Cow-wheat (*Melampyrum cristatum*) displays pale-yellow bracts on its flower-spikes in the Southern Tyrol, but red ones in Lower Austria and Hungary; indeed a long series of plants might still be mentioned which behave in the same way, *i.e.* in which sometimes this sometimes that colour is the more advantageous to the flower, and becomes the prevailing tint in different regions according to the presence of, and in combination with, other plants.

In the descriptions of floral colour, so far given, green has always been regarded as the one which formed the background or substratum from which the other colours and colour-combinations must stand out if they are to be plainly seen by flying animals. As a matter of fact, the ground-tone of the plant-covering during the period of vegetation is mostly green; but in districts where the trees and bushes strip off their foliage in the autumn, and where throughout the winter and spring a mantle of withered leaves covers the ground, the prevailing tint is brown. Similarly, where in the autumn the grasses and various meadow-weeds also wither and fade, the ground-tone of the plant-covered earth in the following spring is not green but pale-yellow or brown. Against such a background obviously the colour-contrasts become somewhat different. Blue colours show up better from a brownish-yellow than from a green background, and it may depend upon this fact that the flowers of so many plants which emerge in spring from the dry withered leaves are coloured blue. The flowers of *Hepatica triloba*, growing in the depths of light woods, are shown up excellently by their blue colour from the yellow-brown Hazel and Hornbeam leafage, but would scarcely be noticed on a green meadow. On ploughed land the flowers of *Omphalodes verna* can be seen 100 yards off over the pale yellow, faded grasses and foliage of the edge of the wood; while at the same distance against a green background they would stand out much less clearly. The same thing is true of many Boragineæ, which grow in similar places (*Pulmonaria angustifolia*, *officinalis*, *Stiriaca*, *Lithospermum purpureo-ceruleum*), of the Lesser Periwinkle (*Vinca minor*), of the Squill (*Scilla bifolia*), and of many others.

Colour-contrasts which differ from those of the green background of land covered with fresh foliage-leaves are also found in shady woodland spots where

dark-brown humus has accumulated. Above the dark mould of the forest-floor a pale colour, such as that of the Bird's Nest (*Neottia*), of *Monotropa*, and of the Toothwort (*Lathræa*), and other saprophytic and parasitic plants, is plainly visible from a distance. These plants would hardly be noticed in a green meadow.

Zoologists are of opinion that animals, especially those which visit flowers to carry off honey and pollen, possess a highly-developed colour sense, and that the visits which are paid by bees, humble-bees, butterflies, flies, and beetles are materially influenced by the colour of the flowers. Different animals prefer different colours, and there are actually certain insects to which some colours are "pleasing", others "unpleasing". The favourite colour of the honey-bee, for example, is a deep violet-blue; pure blue and violet are also pleasing to it, yellow is less sought after but not avoided. Towards green the bees are indifferent, but red is disliked and shunned and is the "unpleasing" colour as far as bees are concerned. With regard to blue and violet it is quite true that these colours in flowers act as excellent allurements for humble-bees and bees, especially for honey-bees, and this is the more remarkable since, as already mentioned, blue flowers are not by any means the most numerous. We can only accept the views of zoologists as to red up to a certain point, however. Flowers with purple-red or carmine-red colour, as well as all the shades from these to violet, are eagerly visited by bees, and therefore only scarlet-red, cinnabar-red, and the shades leading from them to orange are to be regarded as unpleasing to them.

In a garden bed close in front of the house where I live in summer a patch of *Pelargonium zonale*, called by gardeners Scarlet Geranium, is planted. Near at hand, on the other side of the path, there grows the narrow-leaved Willow-herb (*Epilobium angustifolium*). The scarlet-red flowers of the Geranium and the violet flowers of the Willow-herb open simultaneously. Bees and butterflies swarm and flutter hither and thither over them, but, strangely enough, the butterflies halt on both these plants and do not show especial preference for either. The honey-bees fly past the scarlet flowers with indifference, and turn only to the violet flowers of the Willow-herb. In the Vienna Botanic Gardens the bluish-violet flowers of *Monarda fistulosa* and the scarlet *Monarda didyma* stand side by side with the blue flowers of the Hyssop (*Hyssopus officinalis*). All three blossom together about the middle of July. The honey-bees fly about there in large numbers, but they only visit the Hyssop and violet-flowered *Monarda*, the scarlet flowers of *Monarda didyma* being avoided by them. I purposely here say "avoided" and not "disliked", because it is uncertain whether the absence of bee-visits to scarlet flowers is caused really by an actual dislike of the scarlet colour, or whether it is not rather colour-blindness which is known to be the reason why many human beings do not see red. If we say that the honey-bees do not see the scarlet colour it would be clear why they would pay no visits to the flowers of the Scarlet Geranium and the scarlet *Monarda*. They would not notice them, because the nerve-bundles which correspond to the scarlet colour are wanting in their eyes. This does not contradict the fact that other animals see this colour well, and that

for them a scarlet colour may be an effective means of allurements even from a great distance. Butterflies, as already mentioned, hover over the flowers of the Scarlet Geranium; *Monarda didyma* is industriously visited by a large humble-bee, and various animals are seen to fly to other scarlet-red flowers, especially in tropical regions. Such flowers in particular affect the humming-bird. Indeed it seems that this tiny bird in its search after honey prefers scarlet flowers. Perhaps it depends upon this that plants with scarlet flowers are distributed chiefly in those regions where humming-birds have their home. Certainly it is noteworthy that the scarlet colour is only rarely met with in Asia and Europe, particularly in the Alpine, Baltic, Black Sea, and Mediterranean Floras; whilst an exceptionally large number of such flowers occur in America, particularly in Carolina, Texas, Mexico, the West Indies, Brazil, Peru, and Chili. In the primeval forests of Central America every traveller is struck by the great number of Lianes and Epiphytes of the families Acanthaceæ, Bignoniaceæ, Bromeliaceæ, Cyrtandreae, and Gesneraceæ, which bear scarlet flowers, and of which we may mention as examples—*Bignonia venusta*, *Lamprococcus miniatus*, *Pitcairnia flammea*, *Nemanthus Guilleminianus*, *Mitraria coccinea*, and *Beloperone involucrata*. Lobelias, Fuchsias, and Begonias with fiery red cups (*Lobelia cardinalis*, *fulgens*, *graminea*, *splendens*, *Texensis*, *Fuchsia coccinea*, *cylindrica*, *fulgens*, *radicans*, *spectabilis*, *Begonia fuchsoides*, &c.), the scarlet species of Sage which are surrounded by humming-birds (*Salvia coccinea*, *cardinalis*), the various species of *Alonsoa* and *Russelia* belonging to the Scrophulariaceæ, the remarkable Erythrinas (*Erythrina cristagalli*, *herbacea*, *speciosa*), and the Cæsalpinieæ of the genera *Amherstia* and *Brownea* (*Amherstia nobilis*, *Brownea coccinea* and *grandiceps*), whose flowers are so constructed that their honey can hardly be obtained except by the hovering humming-bird—all these find a home in the American regions above-mentioned. Further observations in tropical regions are required to ascertain whether there are not other flower-visiting animals besides humming-birds and butterflies, especially flies and beetles, which can distinguish scarlet flowers and fly to them; for certain plants, as, for example, the Brazilian Aroids with their large scarlet spathes, e.g. *Anthurium Scherzerianum* (the Flamingo Plant), *A. Andrenum* and *Lawrenceanum*, have no honey, and are consequently disregarded by humming-birds and butterflies.

That scarlet flowers are not visited by the hawk-moths, owlet-moths, and other crepuscular and night-flying animals is obvious, since when twilight falls, scarlet, as well as purple-red, violet, and blue flowers become invisible. At this time only those flowers can be seen which are coloured white or yellow on the side turned towards the flying animals, as, for example, the Evening Primrose (*Oenothera*), the Honeysuckle (*Lonicera Caprifolium*), some Nyctagineæ (e.g. *Mirabilis longiflora*), many Solanaceæ (e.g. *Nicotiana affinis*, *Datura Stramonium*), numerous Caryophyllaceæ of the genus *Silene* (e.g. *Silene nutans*, *longiflora*, *Saxifraga*), various species of *Yucca* and *Calonyction*, and, most of all, the large-flowered Mexican Cactuses of the genus *Echinocactus* and *Cereus*, of which the species known as



“Queen of the Night” (*Cereus nycticalus*) is shown in Plate VII. opposite p. 641, vol. i. When dark-coloured flowers are visited at night by insects, for example, those of *Hesperis tristis*, *Pelargonium triste* and *atrum*, it is not in consequence of the colour but of the scent of the flowers, as will be described later on. Without doubt, white is the colour which is not only best seen in the dark, but can be plainly distinguished in bright daylight, and it is, as far as we know, not avoided by a single flower-visiting animal. Even those animals which have a badly-developed sense of colour, and can perhaps only distinguish between light and dark, are able to appreciate white, as it is the lightest of all colours. Yellow flowers are eagerly visited by animals which collect and eat pollen, perhaps because the pollen is usually coloured yellow. Greenish-yellow and brownish-yellow flowers, as, for example, those of the Parsley and the Parsnip, of the Aralia and the Ivy, of the Maple and the Buckthorn, of the Rue and the Sumach (*Petroselinum*, *Pastinaca*, *Aralia*, *Hedera*, *Acer*, *Rhamnus*, *Ruta*, *Rhus*), are especially preferred by flies which swarm over dungheaps and other refuse (e.g. *Lucilia cornicina*, *Onesia sepulcralis*, *Sarcophaga carnaria*, *Scatophaga stercoraria*). This phenomenon has been explained by the similarity of the colours named with those of the dungheap and offal generally. Dark brown must exercise a specially attractive power over wasps. They fly with great haste to brown flowers, especially those whose tint resembles that of decaying pears and other fruit, whilst they will pass by colours which are far more noticeable to other eyes. Flowers of a pale, fawn-red, and dirty violet colour in conjunction with brown, so arranged as to resemble decaying flesh and dead bodies, and such flowers as possess by way of additional attraction a smell of putrefaction, are always visited by carrion-flies and dung-beetles in abundance. It might be thought that the smell alone would suffice to attract these insects; but it must be otherwise, or it is difficult to see why the various Aristolochias, Stapelias, Rafflesias, and Balanophoreæ, which smell like carrion, should bear its colours as well as its scent. It is not easy to decide how much depends upon the colouring, and how much on the scent, and it would be premature to give a definite judgment now. It should be noted generally that the opinions just stated should not be accepted as being entirely free from doubt. Researches on these points are very difficult, and there are so many sources of error that the results may have to undergo many corrections sooner or later. But, on the other hand, all that has been said must not be regarded as quite worthless. This one thing is quite certain—that some animals will show a preference for one colour in a flower, while others will prefer another, and that the absence or presence, the significance or prominence of single floral colours is to be placed on a parallel with the same phenomena in the Animal Kingdom.

It is extremely probable also that in many floral regions the predominance of certain floral colours at various seasons of the year is connected with the distribution of animals in time, since the insects which fly about in spring and summer, and in summer and autumn differ from one another. It has been shown graphically by curves for the region of the Baltic flora that in April and May a white colour predominates, and that from the highest point in May the curve of white gradually

sinks to its lowest point in late autumn. Yellow reaches a first maximum in May, falls somewhat during the summer, and reaches a second maximum in October. The curve of red takes a low position in early spring, rises uniformly through the summer, and reaches its highest point in September. The curves of violet and blue show no large variations through the whole period of vegetation, but two maximal points are to be seen in them, just as in the yellow, one in spring, and the other in autumn.

This particular seasonal change of the prevailing flower-colour, of course, only holds good for the Baltic flora. Even in the adjoining Mediterranean flora the colour-curves are somewhat different, and the deviations are greater still in the flora of corresponding latitudes in North America. Nothing can be said of the predominance of certain colours during the vegetation period in the Alpine flora, for on the heights above the tree-line there is actually no spring and no autumn, only a short summer following a long winter. All the flowers have therefore to blossom in this short time, and all the flower-visiting animals must do their flying about during the short period which is free from snow, if they do not wish to starve. Hardly is the snow melted when there appear almost simultaneously the violet bells of the Soldanellas and the golden flowers of the Cinquefoil (*Soldanella* and *Potentilla*), the white Crowfoot and Androsace, the red Silenes and Primulas (*Ranunculus alpestris*, *Androsace obtusifolia*, *Silene acaulis*, *Primula minima*), the blue Gentians and the yellow Auriculas (*Gentiana acaulis*, *verna*, *Primula Auricula*), the heaven-blue Forget-me-not and the yellow Violet (*Myosotis alpestris*, *Viola biflora*) as well as the Saxifrages in every conceivable colour. On looking at the varied flowers, which have been drawn from nature by E. Heyn at my request, and reproduced in the accompanying Plate XII. entitled "Alpine Flowers in the Tyrol," it will be seen at once that every colour is to be met with here. White and red, yellow and blue, brown and green stand in varied combination side by side on a hand's-breadth of space. The bees, humble-bees, flies, and butterflies which are dependent on the honey and pollen of these flowers may also be seen in Alpine regions flying about at this same time. If one of these animals should be late, its existence is endangered on account of the briefness of the period of vegetation, for should it not happen that some belated flower blossoms in a hollow where the high-piled winter snow has lingered for a long time, the animal is in imminent risk of perishing from lack of food.

#### THE SCENT OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

The scents of flowers, like their colours, are very intimately connected with the Animal Kingdom. The scent of foliage, stems, and roots, as mentioned elsewhere (vol. i. p. 431), serves very efficiently to frighten and ward off herbivorous animals; but the scent emitted from the flowers, on the other hand, serves to allure such animals as transfer the pollen from flower to flower and from plant to plant









ALPINE FLOWERS IN THE TYROL.





by their visits, thus rendering them an important service. In the Auricula (*Primula Auricula*), Woodruff (*Asperula odorata*), Rue (*Ruta graveolens*), and Lavender (*Lavandula vera*), the flowers and foliage have the same scent, and here the insects seeking for honey and pollen are allured to the flowers, whilst the flowers and foliage are protected from being devoured by grazing animals by one and the same substance. A uniform distribution of odorous substance over different parts of the same plant is, however, comparatively rare; much oftener the scent of the flowers differs from that of the foliage. Thus the Garlies (*Allium Chamæmoly*, *Sibiricum*, *suaveolens*) develop the scent of honey in their flowers which brings insects to visit them, while their leaves have a strong odour of onions which keeps grazing animals at bay. In most Umbelliferæ the flowers have a different scent from the foliage-leaves, stem, and roots. The leaves of the Umbelliferous *Euryangium sumbul* (mentioned on p. 745, vol. i.) smell of musk, the root of the Coriander (*Coriandrum sativum*) gives off an offensive odour of bugs, and the Common Hemlock (*Conium maculatum*) has a repulsive odour of mice. And yet the flowers of these three Umbellifers all have a delicate scent of honey, which allures insects to visit them.

The number of scents is very great. At least five hundred can be distinguished. On attempting to classify them and to state their qualities one meets with a serious difficulty, for language is not rich enough to give names to all the different kinds, and nothing remains but to say that Mignonette flowers have a Mignonette scent, Rue flowers have the scent of Rue, and so forth. The need of bringing this multiplicity into something like order, of placing similar scents together and fixing on a central point round which the others could be grouped, as has been done with the ground tints and ground colours, has long been felt, but hitherto sufficient attention could not be given to the need, because the chemical properties of scents which must serve as the basis for any scientific division are only very imperfectly known. However, in what follows the classification of scents which is attempted does not pretend to completeness nor to infallibility, but is to be regarded solely as a first attempt or preliminary outline to which one can turn provisionally in the naming these scents.

Five groups of floral scents may be conveniently distinguished, *i.e.* the indoloid, aminoid, paraffinoid, benzoloid, and terpenoid scents.

To the first group, the *indoloid* scents, belong those volatile substances which arise from the decomposition of albuminous compounds and diffuse into the atmosphere, and in which one or several benzole nuclei are retained, as well as nitrogen; examples are Leucin and Tyrosin, Skatol and Indol. The group derives its name from the last-named substance. These are developed in the inflorescences of numerous Aroids, in the flowers of all the South African Stapelias, in those of the Balanophoreæ, Rafflesiaceæ, and Hydnoreæ, in the perianths of about 200 Aristolochias, and also in those of some tropical Orchids, as, *e.g.* of *Bolbophyllum Beccarii* of the Malayan flora. Sometimes the scent resembles that of decomposing mammalian flesh, sometimes of rotten fish (*cf.* vol. i. p. 196), sometimes again of decom-

posing animal excreta. The West Indian *Aristolochia Gigas* has the scent of old decaying tobacco, and the red-brown flowers of *Calycanthus* smell like fermenting wine, quite unlike the woody branches, which have a pleasant odour reminding one of cloves. It has already been stated that flowers provided with indoloid scents resemble animal corpses in their colouring, having usually livid spots, violet streaks, and red-brown veins on a greenish or fawn-coloured background.

The *aminoid* scents come next to the indoloid. Under this name are comprised all those volatile substances which diffuse into the air and have an amine as their foundation, either a primary, secondary, or tertiary amine, according as to whether one, two, or all three of the hydrogen atoms of the ammonia are replaced by an alcohol radical. It has been shown that the curious odour of the Hawthorn (*Cratægus*) is due to trimethylamine. It is very probable that in numerous other flowers with similar scent trimethylamine or a related compound—ammonia—is developed. The smell of Hawthorn flowers is repeated with slight modifications in the flower of the Pear (*Pyrus*), the Medlar (*Mespilus*), the Mountain Ash (*Sorbus*), the shrubby Spiræas (*Spiræa ulmifolia*, *chamædryfolia*, &c.), the Dogwood (*Cornus sanguinea*), the Wayfaring Tree and Guelder-rose (*Viburnum Lantana*, *Opulus*), the Chestnut (*Castanea*), the Elder (*Sambucus racemosa*), the Traveller's Joy (*Clematis Vitalba*), and the Barberry (*Berberis*). The scent which is liberated from the flowers of the Tree of Heaven (*Ailanthus*), of the Horse-chestnut (*Æsculus Hippocastanum*), of the Flowering Ash (*Fraxinus Ornus*), and of the Evening Primrose (*Oenothera*), resembles that of *Cratægus* more remotely. The flowers of the Ivy (*Hedera*) develop a scent which reminds one of herring-pickle, those of the Alpine Poppy (*Papaver alpinum*), partly of Hawthorn, partly of Musk. Two North American plants, viz. *Pachysandra* and *Sanguinaria*, produce a scent distantly resembling ammonia which proceeds, apparently, from an amine compound. Under this division, finally, should be placed that odour so repulsive to the human olfactory organ which is produced by the flowers of the already-mentioned *Melianthus* (see p. 171).

The third group, that of the *benzoloid* scents, is composed of such as are formed from the so-called aromatic bodies. They are compounds with a benzole nucleus in which the various hydrogens of the benzole are replaced by alcohol and acid radicals. The Eugenol (or oil of cloves) in the flowers of many Pinks (*Dianthus Caryophyllus*, *plumarius*, *superbus*), the Cinnamyl-alcohol which smells like Hyacinths, the Salicylic aldehyde in the flowers of the Meadow-sweet (*Spiræa Ulmaria*), the Coumarin in the flowers of the Woodruff (*Asperula odorata*), the Vanilla-like scent in the flowers of the Heliotrope (*Heliotropium*) are all well-known chemical compounds. I would also include with these the scents of the Lilac (*Syringa vulgaris*), Lily of the Valley (*Convallaria majalis*), Mignonette (*Reseda odorata*), Jessamine (*Jasminum officinale*), Auricula (*Primula Auricula*), Honeysuckle (*Lonicera Caprifolium*), Acacia (*Robinia Pseudacacia*), Violet (*Viola odorata*), Cyclamen (*Cyclamen Europæum*), Paulownia (*Paulownia imperialis*), and of Ilang-Ilang (*Cananga odorata*).

It is very remarkable that many of these benzoloid scents are repeated in species of very different plant-families. Clove-scent is apparent not only in the above-named Pinks but also in the flowers of many species of Broom-rape (*Orobancha caryophyllacea*, *gracilis*, *lucorum*), in some Orchids (e.g. *Habenaria bifolia*, *Gymnadenia conopsea*), in the yellow flowers of *Ribes aureum*, in the Narcissus (*Narcissus poeticus*), and in a somewhat modified form in the flowers of *Azalea pontica*. Many Catchflies (*Silene nutans*, *longiflora*, &c.), the Dame's Violet (*Hesperis tristis*), and the dark-flowered Pelargoniums (*Pelargonium atrum*, *gauciifolium*, *triste*, &c.) develop the scent of Hyacinth flowers. It has long been known that the scent of Woodruff is found in the flowers of many Grasses (*Anthoxanthum*, *Hierochloa*), and mixed with honey-scent in the flowers of the Melilot (*Melilotus*). The scent of Vanilla is very widely distributed. Besides the Heliotrope (*Heliotropium Europæum* and *Peruvianum*) some species of Woodruff (e.g. *Asperula glomerata*, *cynanchica*, *longiflora*), the Linnæa (*Linnæa borealis*), the Dwarf Elder (*Sambucus Ebulus*), the small Bindweed (*Convolvulus arvensis*), some Orchids of our upland and alpine meadows (e.g. *Gymnadenia odoratissima*, *Nigritella nigra*), the alpine Saussurea (*Saussurea alpina*), the alpine Spurge Laurel (*Daphne alpina*), and the Nardosmia (*Nardosmia fragrans*) are provided with vanilla-scent to a greater or less degree. Different, but still resembling Vanilla, is the scent of tropical Orchids of the genus *Stanhopea*, and the exactly similar scent of *Epipogium aphyllum*, which grows in European Pine-forests. Lilac scent is less common, but it is found clearly enough in many allies of the Spurge Laurel (e.g. *Daphne striata* and *pontica*). This is the more strange, since the flowers of these Daphnes, though not even related to the Lilac, resemble Lilac flowers to a surprising extent at first sight. On the other hand, many species of the genus *Syringa*, e.g. *Syringa Emodi*, which grows on the Himalayas, have a scent which differs from that of *Syringa vulgaris* (the Lilac). The Lily of the Valley scent is on the whole rarely met with—only in some Mexican Cactuses, especially in *Echinocactus Tetani*. Acacia scent is found in a good many Papilionaceæ, as, for example, in *Cladrastis lutea*, *Cytisus alpinus*, and *Spartium junceum*, and also in the flowers of an Iris (*Iris odoratissima*). Auricula scent, besides in many Primulas allied to *Primula Auricula*, is present in the flowers of the Globe-flower (*Trollius Europæus*). Honeysuckle scent is emitted in the evening from the flowers of all the species allied to *Lonicera Caprifolium*, and also in the flowers of *Ismene*, and of a species of Tobacco (*Nicotiana affinis*). Violet scent is fairly widely distributed. In addition to numerous species of Violet (e.g. *Viola odorata*, *mirabilis*, *polychroma*) it is also developed in many Cruciferæ, thus, in the Stocks (*Matthiola annua*, *incana*, *varia*, &c.), in the Wallflower (*Cheiranthus Cheiri*), and in the common Dame's Violet (*Hesperis matronalis*). The Snowflake (*Leucojum vernum*), the autumn-flowering fringed Gentian (*Gentiana ciliata*), the Spurge Laurel (*Daphne Laureola* and *Philippi*), the blue Water-lily of the Nile (*Nymphæa cœrulea*), and the insectivorous Sarracenia (*Sarracenia purpurea*) emit an unmistakable scent of Violets from their flowers. Cyclamen scent is again



found in the flowers of a Winter-green (*Pyrola uniflora*); *Paulownia* scent in the flowers of *Glycine Chinensis*; and *Unona* scent in the flowers of *Zaluzianskia lychnidea*.

The acids and alcohols of those hydrocarbons which are known as paraffins differ chemically from the benzoloid scents. The name *paraffinoid* may be given to them. With regard to their composition the best known of these compounds are Valerianic acid yielded by the Valerian scent in the flowers of numerous Valerians, especially of *Valeriana officinalis*, *montana*, and *saxatilis*; Pelargonic acid, which is closely connected with Rose scents, and especially with that of *Rosa centifolia*; the Oil of Rue which is liberated from the flowers of various Rutaceæ, especially of the Common Rue (*Ruta graveolens*); and the volatile Ceanthic acid which is met with as the wine-flower scent in the flowers of the Vine (*Vitis vinifera*), and of Gleditschias (*Gleditschia triacanthos*, *Sinensis*, &c.). To this group belong also the Lime scent which diffuses with various modifications from the flowers of different Limes (*Tilia alba*, *Americana*, *parvifolia*, &c.), and also from those of *Æsculus macrostachya*; the very widely-distributed Nightshade scent from the flowers of many species of the Thorn-apple (*Datura*), of the Mandrake (*Mandragora*), the *Petunia* and numerous other Solanaceæ, as also from those of the Peony (*Pæonia*), and American *Trillium grandiflorum*. The Elder scent of the flowers of *Sambucus nigra* and *Orchis pallens*, and the hircine odour, resembling caproic acid, which is liberated from the flowers of the Lizard orchis (*Orchis hircina*), and, somewhat modified, from those of *Orchis fragrans* are also to be included.

It is uncertain whether the honey scent of fresh yellow bees'-wax and honey developed in so many flowers belongs to the paraffinoid series or not. Formerly it was thought that myricilalcohol (an alcohol of paraffin) caused this peculiar scent. But it would appear that the purified myricilalcohol is scentless, so that it is therefore possible that the honey scent is due to another compound. At any rate, it is naturally associated with the above-mentioned scents, and can be most conveniently described here. It is a very common, if not the commonest of all flower scents. The fact that it is often combined with others, especially with benzoloids, leads to the formation of many varieties. The scent, which is most like that of honey-filled honey-comb fresh from the hive, is produced by the flowers of the Sloe, Apricot, Cherry, and Almond trees (*Prunus spinosa*, *Armeniaca*, *avium*, *Amygdalus communis*, &c.), of *Herminium*, belonging to the Orchids, of the Buckthorn (*Rhamnus pumila*, &c.), and of the Bugwort (*Cimicifuga fætida*). A slightly different scent is liberated by the flowers of the Bird Cherry (*Prunus Padus*), the Bedstraws (*Galium Cruciata*, *vernum*, *verum*), of the alpine Forget-me-not (*Myosotis alpestris*), and Phlox (*Phlox paniculata*), of *Asclepias* and *Cynanchum*, the Corydalis (*Corydalis cava*), many species of Spurge (*Euphorbia Cyparissias*, &c.), the Willows (*Salix Caprea*, *daphnoides*, &c.), some Compositæ (e.g. *Cirsium arvense* and *brachycephalum*), numerous Umbelliferæ (e.g. *Angelica officinalis*, *Heracleum Sphondylium*, *Meum Mutellina*, *Pimpinella magna*), many Cruciferæ (e.g. *Alyssum montanum*, *Erysimum odoratum*), many Tulips and

Garlics (*Tulipa sylvestris*, *Allium Sibiricum*, *Chamæmoly*, &c.), of the Buckwheat (*Polygonum Fagopyrum*), and of many others. The sweet scent of the Clover which occurs in species other than the common meadow Clover (*Trifolium pratense*) and in other Papilionaceæ (e.g. *Trifolium resupinatum*, *Lathyrus odoratus*) is only a form of honey-scent.

The last group consists of scents produced from ethereal oils destitute of oxygen called terpenes; the scents corresponding to them may therefore be called *terpenoids*. The materials which give rise to these scents are found sometimes in special receptacles imbedded in the plant-tissues, sometimes in the enlarged end-cells of the so-called glandular or capitate hairs—for the most part in the region of the stem and foliage, more rarely in the flowers. The best-known terpenoid scent occurring in flowers is that of the Orange-flower, produced by Oil of Neroli, which is obtained by distillation of the flowers of *Citrus Aurantium*; in those of Gardenias (*Gardenia*), of *Pittosporum Tobira*, of the Siberian *Pyrus baccata*, and somewhat modified in the flowers of some Magnolias (e.g. *Magnolia obovata* and *Yulan*); also the Citron scent from Oil of Citron which occurs in the flowers of some species of Thyme (*Thymus citriodorus*, *montanus*, &c.), more especially in those of Fraxinella (*Dictamnus Fraxinella*), and the scent of Lavender which is produced from the Oil of Lavender present not only in the foliage but also in the flowers of *Lavandula*.

It has already been incidentally mentioned that two kinds of scent are often liberated simultaneously from the same flower, and that the scent of honey, in particular, frequently combines with some other. The identification of the scent is rendered much more difficult under these circumstances, especially as sometimes one, sometimes the other scent predominates according to the time of day. Not unfrequently one hears wholly different opinions about the scent of a flower. One observer thinks it to be vanilla, perhaps, another a violet scent. Both may be right, since two kinds of scent may be actually liberated from the same flower, whilst individuals are frequently unequally susceptible to all odours.

The difficulties of identifying the flower scent are also increased by the fact that a certain amount of imagination is almost unavoidable. Taste and sight may also be at fault. On looking at a Carnation one is immediately reminded of the smell of cloves before the scent has actually reached the nose. It is therefore advisable that the flowers should not be seen while their scent is being identified, and that to examine them one should get a friend to hold them before one's nose after one's eyes are shut.

It is noticeable that similar and closely-allied species of plants often have different scents. Many examples have already been given, amongst others that *Gymnadenia conopsea* has the smell of cloves, and the very similar *Gymnadenia odoratissima* a vanilla scent. Of species of the genus *Daphne*, *Daphne alpina* has a vanilla scent, *Daphne striata* a lilac scent, *Daphne Philippi* a scent of violets, and *Daphne Blagayana* a clove scent. The closely-allied *Orehis fragrans* and *coriophora* can be at once distinguished by the smell of their flowers. The scents

occurring in different species of *Syringa*, *Tilia*, and *Sambucus* can also be easily recognized. In Roses this phenomenon is even more remarkable. From their scents *Rosa alpina*, *pimpinellifolia*, *arvensis*, *Indica*, *moschata*, *canina*, *Gallica*, *cinnamomea*, *Centifolia*, and *Thea* can be at once distinguished with closed eyes by anyone who has examined the numerous species of this genus even to a limited extent. It is also remarkable that in closely-allied species the flowers of one will smell while those of another will be scentless. *Habenaria montana* has no scent, whilst *Habenaria bifolia* exhales a strong scent of cloves. *Viola tricolor* is scentless, *Viola polychroma* develops a strong violet scent. The flowers of *Primula Lehmanni* have no scent, while those of *Primula Auricula*, which can hardly be distinguished from the former, have a strong Auricula smell. These facts are not without bearing in the theory of specific constitution of protoplasm, as will be discussed later on in the chapter on the Origin of Species, and therefore should be noted here in passing.

We are liable to many erroneous inferences with regard to the perception of flower scent by animals, since our judgment depends mainly on our own sense of smell, and it is very possible, even probable, that the power of smell in flower-visiting animals differs materially from ours. The olfactory sense of man is lodged in a sharply-defined portion of mucous membrane in the upper part of the nasal cavity. There the superficial cells of the mucous membrane join with the end branches of the olfactory nerve in a peculiar net-work, and the scents must act directly on this region if they are to produce the sensation of smell. But this is again only possible if the odorous substances give off fine particles into the air, and if this impregnated air is wafted over the special part of the nasal mucous membrane. It was formerly held that the substances passing thus over the olfactory mucous membrane were dissolved in a fluid and were then distributed in solution. Only in this way could they influence the nerve-endings. But this view is contradicted by a series of facts of which the most important are the following: it is well known that we can smell certain metals whose finely-divided particles break away and enter the nose, although these metals are certainly not soluble in the mucous membrane. We are also able to smell very different scents quickly, one after the other, which would not be the case if the sense of smell were dependent on a previous solution of the odorous substance in the fluid which saturates the mucous membrane. Again it is a remarkable fact that the mucous membrane is altogether absent from the olfactory organ of many animals. The knobs and pegs on the surface of the feelers which form the olfactory organs of insects are indeed connected on one side with gangliose nerve-endings, but they have nothing resembling a mucous membrane which could contain or secrete a fluid, and yet insects are characterized by their fine sense of smell.

The stimulation of the nerve-endings in the olfactory organ cannot therefore be the result of a previous solution of the odoriferous substance, but must be considered as the transference of a movement. It seems as if the molecules of the odorous substance which are present in the air undergo a rotatory, vibrating, or



some kind of swinging movement, and that this movement is transferred to the nerve-endings as soon as the molecules come into contact with the olfactory organ. Since the nerve-endings are not exposed the transference must take place through the portion overlying the nerve-ends, and it must depend upon the structure of this superficial layer which is exposed to the air whether the transference takes place quickly or slowly, completely or only partially. It is necessary that the stimulation of the nerve-endings, which we imagine to be a form of movement, should be conducted to the central organ if it is to be perceived as smell. But now arises this difficult question: Do the various sensations of smell depend upon the fact that different nerve-endings are stimulated by different odorous substances, and that a particular scent, *e.g.* that of Oil of Lavender, is only perceived when those particular nerve-ends are stimulated which are sensitive to the kind of vibration undergone by the molecules of the Oil of Lavender? Or, are they caused directly by the movement of the molecules of any odorous substance being transmitted by any olfactory nerve-fibre to the central organ, and there producing a definite sense of smell? In this case the same nerve-fibre which had just transmitted the vibrations of the lavender oil would be capable in the next moment of transferring to the central organ those belonging to the molecules of chloroform.

The one hypothesis assumes that certain parts of the central organ, as well as the nerve-fibres leading to them, differ essentially from one another in their capability of being stimulated, although they seem to our senses to be of exactly the same structure. One part can only be stimulated by Oil of Lavender and is not affected by chloroform molecules, another part is only set into a corresponding movement by the swinging of chloroform molecules, but is not in sympathy with the particular movement of those of lavender oil. But to favour this hypothesis is to assume an enormously large number of different nerve-endings in the olfactory organ considering the innumerable quantity of different odoriferous substances that exist—even if it be granted that there is a place only for groups of similar substances in the olfactory organ and not for each singly, the individual scents of each group being only produced by the different degree of the stimulation. The other hypothesis assumes that each olfactory nerve-fibre according to its structure is enabled to transmit the different forms of movement which occur at its peripheral end to the central organ. The particular movements of the molecules of lavender oil would not only affect the nerve-ends, but would continue as a specific form of movement through the whole nerve-fibre to the central organ, and would be there perceived as the scent of lavender oil. This same nerve-fibre which had just transmitted the scent of lavender might in the next moment transmit the vibrations of chloroform and produce the chloroform smell. Such conduction resembles that of a telephone at least in this that different words spoken at one end through the same telephone can be heard unaltered at the other end. The assumption of a conduction of specific forms of movement set up by odorous substances from the periphery through the whole nerve-fibre up to the central organ, also renders it necessary to assume that the olfactory nerve-fibres are not stimulated at all by

certain materials. Thus vibrations which exceed the limits of irritability of the olfactory nerves in rapidity produce no smell.

Whichever hypothesis one accepts one comes to the conclusion that a great difference may exist between the sense of smell of men and animals according to the different degree of sensitiveness of their olfactory fibres. Although the molecules of a substance floating in the air stimulate (*i.e.* set in motion) no single nerve-ending in the human olfactory mucous membrane, this does not prove the absence of nerves in the olfactory organ of some animal sensitive to the particular form of motion of these molecules. It might easily happen that one insect would smell Hyacinths but not Roses, while another would smell Roses and not Hyacinths. This conclusion is, however, of importance in explaining the allurements of certain animals to flowers which appear scentless to man, as well as in explaining the phenomenon that many flowers are eagerly visited by one group of insects and are avoided or rather ignored by another. The Virginian Creeper, *Ampelopsis quinquefolia*, so often planted to cover porches, palings, and walls, develops flowers in midsummer which are visited by bees very industriously and eagerly. The colour does not act as an allurements in this case, for the flowers have green corollas, are hidden away under the foliage, and cannot be seen even by good eyes at a little distance. Yet the bees fly thither from all sides in such a way as to leave no doubt that the flowers of the *Ampelopsis* can be perceived by them a considerable way off. Since it is not their appearance it must be their smell which announces their presence! But to men they appear to be quite scentless! The flowers of the Common Bryony (*Bryonia dioica*) are not less remarkable. They occur on two kinds of plants, *i.e.* on one plant are developed only staminate and on the other only pistillate flowers, and since the pollen is not powdery, and therefore not scattered by wind, it must be carried by insects from plant to plant if the ovules are to mature. But the flowers, especially the pistillate ones, are very insignificant, green in colour, with faint smell, and they are half hidden under the foliage. Many insects fly past them without noticing them. They are almost exclusively visited by one of the Hymenoptera, viz. *Andrena florea*, and it can find them even in the most out-of-the-way places. This can hardly be accounted for except by supposing that the scent of Bryony flowers is perceived by these particular bees and not by other insects. To these two examples of insignificant flowers, which appear to men and to many animals to be scentless but which are nevertheless eagerly tracked by certain insects, may be added the common Birthwort (*Aristolochia Clematidis*), the Whortleberry (*Vaccinium Myrtillus*), *Chamaeorchis alpina*, the Twayblade (*Listera ovata*), and many others. It is probable that there are also flowers which differ from these in having bright colours contrasting with the green foliage, and in addition exhale a special scent to allure certain animals. It is, of course, hardly possible to speak with certainty. In all these questions we have to deal with observations concerning the relations between insects and flowers in nature, and since many sources of error exist, the conclusions arrived at must be accepted with discretion. As to the so-called "flower fidelity"

of insects, by which is meant the preference of certain kinds for certain flowers, the matter is only mentioned here very generally so far as the scents are concerned, and only the main results of these observations are given.

It may be stated as one of these that the indoloid scents have an attraction for certain flies of the genera *Scatophaga*, *Sarcophaga*, *Onesia*, *Lucilia*, *Pyrellia*, *Calliphora*, *Sepsis*, and *Musca*, and for beetles of the genera *Aleochara*, *Dermestes*, and *Saprinus*, which appear on carrion and excrement; indoloid scents remain unnoticed, on the other hand, by butterflies, bees, and humble-bees. Aminoid scents attract large and small beetles, especially Cetonias, and after them Hymenoptera; butterflies, however, are hardly ever allured by them. The scent of honey acts powerfully on bees and humble-bees; also on butterflies, burnet-moths (*Zygæna*), and on day-flying hawk-moths (e.g. the Humming-bird Hawk-moth, *Macroglossa stellatarum*), as well as on small beetles; but insects which are attracted by indoloid scents are not affected by the scent of honey. Certain Hymenoptera which, oddly enough, themselves have paraffinoid scents (viz. species of *Prosopis*), fly to flowers with the same smell. Flowers with the scent of Honeysuckle are frequented by large crepuscular hawk-moths, but this scent has no attraction for beetles. Butterflies will pass over flowers with a Honeysuckle scent without pausing, leading us to think that either the scent is not perceived by them, or that they find it unpleasant.

Many flower scents, especially the paraffinoids, are less easily perceived at their place of origin than at a little distance, which is explained by supposing that the odorous particles liberated from the flowers are acted on by oxygen or aqueous vapour as they diffuse through the air, and that various molecular changes go on in them. But since our knowledge of the chemical properties of scents is still so imperfect we must beware of suppositions of this kind. The phenomenon is most pronounced in the Lime and in the Vine. As one approaches a Lime-tree in full flower the pleasant scent of its blossom is strongest at a distance of about 30 yards; if one comes into the immediate neighbourhood and smells the flowers on its lower branches, the scent is neither so strong nor so pleasant as it was further off. In a journey up the Danube, through the part of the valley called the Wachan, with its Vine-clad slopes, I found the air of the whole valley, even that above the water, so filled with the scent of Vine flowers that it seemed almost impossible they should be so far off. And yet the nearest Vines on the banks were 100 yards above the water, and at least 300 yards from the boat. Afterwards I found when wandering through the vineyards that the smell of the flowers close at hand was much weaker than at a distance, and was forced to the paradoxical opinion that with increasing distance and diffusion over a wider area the scent does not diminish but waxes stronger.

The fact that man can perceive certain odoriferous substances in the finest state of division and at incredible distances paves the way for explaining the so-called animal perception of scents. We speak of this animal perception when we gather from other signs that an animal is able to smell what we cannot at the same



distance. Since it has been already explained that animals can perceive scents which will not stimulate our olfactory nerves at all, it is not wonderful that bees will fly from a distance to the flowers of *Ampelopsis*, although they are not able to see these flowers so far away. They smell the flowers of *Ampelopsis* which are scentless to us at 300 yards, just as we do the flowers of the Vine at the same distance.

Of the multitude of remarkable observations concerning the power of smell in animals only those interest us here which are connected with the visits of insects to flowers; of these, two deserve special mention. Some years ago the Aroid *Dracunculus Creticus* from Cyprus was planted on the edge of a small group of coniferous plants in the Vienna Botanic Gardens. There was no dungheap or decomposing animal matter anywhere in the vicinity, nor was there any trace of carrion-flies or beetles. But when during the summer the large cornet-shaped flower-sheath of this Aroid opened, innumerable carrion-flies and dung-beetles flew thither at once from all sides. The indoloid scent emanating from the flower-sheath was only noticeable by human beings a few yards off, but the animals named must have smelt it many hundred yards away. In a certain part of this same garden there is a plant of Honeysuckle (*Lonicera Caprifolium*), and in summer when twilight falls this is regularly visited by the Convolvulus Hawk-moth (*Sphinx Convolvuli*). These hawk-moths are accustomed, after they have sucked the honey and when the twilight fades into night, to settle near the plant on the bark of old tree-trunks or on fallen leaves, and there they remain with folded wings as if they were benumbed until the next evening. A few summers ago I very carefully picked up one of the pieces of wood which had been chosen as a resting-place by one of these hawk-moths. I marked the moth slightly with cinnabar and brought it, together with the piece of wood on which it remained immovable, to another part of the gardens 300 yards away from the Honeysuckle. When twilight fell the hawk-moth began to wave the feelers which serve it as olfactory organs hither and thither a few times, then stretched its wings and flew like an arrow through the garden towards the Honeysuckle. Shortly after I met the hawk-moth with the cinnabar mark hovering over these flowers and sucking the honey. It had flown straight to the plant, and must have been able to smell the scent of the flowers even at so great a distance.

One of the most remarkable correlations between flower scent and animals is the development of the scent simultaneously with the time of flying of certain insects. The flowers of certain species of Honeysuckle, which are much visited by crepuscular Lepidoptera (*Lonicera Caprifolium*, *Peridymenum*, *Etrusca*, *grata*, &c.), of Petunias (*Petunia violacea*, *viscosa*, &c.), of *Habenaria bifolia*, and of many other plants, smell very faintly or not at all through the day. After sunset, from about 6 or 7 in the evening until midnight, they give off an abundant odour. Still stranger is the behaviour of the flowers of *Hesperis tristis*, of the dark-flowered Pelargoniums (*Pelargonium triste*, *atrum*, &c.), and of numerous Caryophyllaceous plants (*Silene longiflora*, *nutans*, *viridiflora*, &c.), which are visited by

small nocturnal moths, and give off no scent during the day, but exhale a strong Hyacinth odour at twilight. Similarly the flowers of the common Dame's Violet (*Hesperis matronalis*) smell like Violets in the evening, and those of a species of Woodruff (*Asperula capitata*) smell of vanilla as darkness approaches. On the other hand, many flowers visited during the day by butterflies, bees, and humble-bees become scentless at sunset. The yellow flowers of *Spartium scoparium* only exhale their exquisite acacia scent when the sun is high and the insects named are swarming through the warm air. In the evening there is no trace of the scent. The ornamental Clover, *Trifolium resupinatum*, whose flowers are surrounded by bees, smell strongly of honey in the sunshine, but become scentless as soon as the bees return to their hive at twilight. The same is true of the Grass of Parnassus (*Parnassia palustris*), which only smells of honey in bright sunshine and becomes scentless in the evening. A species of Daphne growing in the Pyrenees (*Daphne Philippi*) liberates a delicate scent of Violets during the day, only ceasing to smell when night falls.

It is sometimes suggested that colour and scent in flowers to some extent mutually exclude one another, so that in cases where the allurements of honey- and pollen-eating insects is brought about by the bright colour of the corolla, the scent is absent, and *vice versa*. This idea is supported by the facts that many flowers with brilliant colouring, which can easily be seen at a distance on account of their large size, have no scent, *e.g.* the flowers of the Cornflower (*Centaurea Cyanus*), the Pheasant's Eye (*Adonis vernalis* and *flammea*), many Gentians (*Gentiana acaulis*, *Bavarica*, *verna*), various species of Lousewort (*Pedicularis incarnata*, *rostrata*, &c.), the Camellia (*Camellia Japonica*), the Indian Azalea (*Azalea Indica*), and numerous species of *Amaryllis* and *Hemerocallis*; whilst, on the other hand, many plants with small and insignificant flowers, as, for example, the Mignonette (*Reseda odorata*), the Vine (*Vitis vinifera*), the Ivy (*Hedera Helix*), Gleditschia (*Gleditschia triacanthos*), and Eleagnus (*Eleagnus angustifolia*) give off a strong scent which can be perceived at some distance. It might be also pointed out that the oft-mentioned Pelargoniums (*Pelargonium atrum* and *triste*) and *Hesperis tristis*, which bear dirty yellow and dark flowers, indistinguishable to the best sight in twilight, develop a strong Hyacinth odour, which allures numerous small night-flying Lepidoptera. But however conclusive these examples may be, there are many others of the opposite kind, *i.e.* of bright and noticeable colours, occurring not infrequently in conjunction with strong scents. Roses, Pinks, and Stocks, many tropical Orchids, Magnolias, Narcissi and the large-flowered Rhododendrons of the Himalayas show at least that the view mentioned has not a universal application.

## OPENING OF THE PASSAGE TO THE INTERIOR OF THE FLOWER.

The removal and transmission of pollen by animals can obviously only take place when the perianth-leaves, under whose protection the pollen and stigmas are matured, permit of access to the base of the flower. I have altered the usual

expression "Opening of Flowers" in the headline above, since flowers exist to which the term "open" does not apply. The flowers of the Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) never open spontaneously; but the insects which frequent them for honey have to open the door for themselves by pushing down the lower lip. So, also, in the flowers of Papilionaceæ. In the bud the uppermost petal or standard incloses the four others like a mantle; only when the pollen is mature, and has been discharged from the anthers, does the standard fold back, and one says the plant is in flower. But still no opening is to be seen, access to the honey remains now, as before, hidden, and insects must introduce their probosces between the folded petals. Still, from a consideration of these and other cases, it may be urged that there is essentially an opening of what was closed in the bud, a giving of access to the interior of the flower, so that perhaps the headline above meets the case.

The arrangement of the petals in the flower-bud is determinate for individual cases, and is often made use of by descriptive botanists as a useful character for discriminating families and genera. This manner of folding is known as *Æstivation*, of which several forms are distinguished. (1) The *crumpled* æstivation, characteristic of the Poppy, Cistus, and Pomegranate (*Papaver*, *Cistus*, and *Punica*). The petals here, to quote Grew, "are cramb'd up within the *Empalement* [i.e. calyx] by hundreds of little *Wrinkles* or *Puckers*; as if Three or Four fine *Cambrick Handkerchiefs* were thrust into ones *Pocket*". (2) *Plaited* or *plicate* æstivation, where a funnel- or bell-shaped corolla is folded in regular, longitudinal pleats, as in Venus's Looking-glass (*Specularia*). (3) When the band-like corollas of many Composites, as the Salsify and Dandelion (*Tragopogon* and *Taraxacum*) are rolled up longitudinally into a tube closed above by five little teeth, one speaks of a *convolute* æstivation; (4) when, as in Umbelliferæ and many Caryophyllaceæ, the petals are rolled up from apex to base, of a *circinate* æstivation. (5) Sometimes the folded or unfolded petals are so placed one upon the other, that on one side each is in contact with the adjacent petal of that side, and on the other side with that of the other, the whole corolla appearing spirally twisted. This condition is known as *contorted* æstivation, of which examples are the Wood-sorrel (*Oxalis*), Periwinkle (*Vinca*), and other Apocynaceæ, Solanaceæ, and Convolvulaceæ. (6) The commonest form of æstivation is that in which the petals or lobes of a united corolla overlap like tiles on a roof, without being twisted, however. The outmost petal covers all the rest, or a pair of outer petals inclose a pair of inner ones. This, the *imbricate* æstivation, is characteristic of the Apple, Rose, Buttercup, and Anemone, also, in a modified form, of Papilionaceæ and Pinks. (7) In a number of plants, e.g. *Asarum*, Lilac, and Vine, the petals do not overlap, but touch merely by their margins, and form a sort of dome or vault. This is known as *valvate* æstivation. Among these kinds of æstivation various combinations occur, thus the Poppy in addition to being crumpled is imbricate, and several Pinks (*Dianthus neglectus*, *glacialis*, &c.) with imbricating petals are also convolute. It further often happens that the leaves of the calyx have an æstivation differing from that of the corolla. Here, again, the Poppy is an instance in point, its calyx is valvate, and its corolla imbricate and crumpled.



In bilabiate corollas, although the individual parts vary a good deal, the imbricate æstivation is constant, though numerous modifications obtain which cannot be described at length here. Two fairly frequent cases, however, must be described, appertaining to the ringent and personate corollas, to be referred to by and by. In the ringent corolla the upwardly-bent median lobe of the lower lip is placed like a lid in front of the corolla-tube, and upon it lie the two lateral lobes of the same lip; these are covered by the downwardly bent upper lip. In the buds of the Germander (*Teucrium*), the middle lobe of the lower lip is bent up to such an extent that it covers over the anthers like a dome, whilst in those of the flowers of the scrophularineous Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) complete closure of the flower is caused by an inflated portion of the lower lip (the so-called palate), this is covered by the upwardly-directed, central lobe of the lower lip, and this again by the two downwardly directed lobes of the upper lip.

All these obstacles, however, to access to the interior of the flower are soon removed. The petals, having served as protective wrappers to the bud, fall away on the opening of the flower in cases where they have no further function to discharge. This condition, truly, is a rare one, but occurs in the Vine (*Vitis*). The petals here are valvate in the bud and form a dome-like covering to the stamens and ovary; they are green in colour, not readily distinguishable from the foliage, and of little value as attractive organs for insects. Under these circumstances it is of advantage that they should be got rid of quickly. This is accomplished as follows. The petals separate from the flower at the base, each rolls up spirally, and they remain hanging together by their apices for a while like a hood, which is ultimately thrown off in consequence of the expansion of the stamens.

This class of opening of flowers is, as stated, rare. In the great majority of cases the petals play a definite part in the later stages of flowering, and are consequently retained. Access to the interior of the flower is brought about by the development between the petals of wide slits as in the Rampion (*Phyteuma*), or, in ordinary cases, by the entire separation of their free ends from one another; the petals, in fact, spread out, and sometimes even become folded back. This separation, of course, corresponds to the position which the petals previously occupied in the bud. Where the æstivation is valvate, the apices of the petals simply fold back like valves; where it is imbricate, the petals become disentangled; where it is plaited or crumpled, the folds or inequalities become smoothed out. Spirally-twisted buds become untwisted, and it may frequently be observed that two or even three different sorts of movement are necessary for a flower to open.

In this way, in many cases, only a somewhat circumscribed opening arises, leading down to the expanded or tubular interior portion of the flower. In others, again, the whole flower opens widely like a cup or saucer, as in Roses, Anemones, and Peonies.

The separation of the petals usually happens very quickly. In the Honeysuckle (*Lonicera Caprifolium*) opening begins with the folding back of the lowest lobe of the corolla, followed by a similar movement of the others, the stamens become liberated and spread like the fingers of a hand. The whole series of movements can

be readily followed, and lasts barely two minutes. Still more rapid is the opening of the Evening Primrose (*Oenothera grandiflora*). The petals spring apart quite suddenly and stretch themselves out within half a minute. If ever the term "bursting open" applies to a flower-bud, it does so here. In several tropical Orchids, also, the parts separate quickly enough for the movements to be readily visible. Thus, in the beautiful *Stanhopea tigrina*, the whole process only occupies three minutes. It is worth mentioning, that during the opening of this flower, a distinct noise is heard, not unlike the report caused by the bursting of the inflated calyx of the Bladder-campion.

There are flowers which open so early in the morning that they greet the first rays of the rising sun with fully expanded corollas. That common garden climber, *Ipomœa purpurea*, opens its buds at 4 a.m. Wild Roses, also, open between 4 and 5 a.m. Between 5 and 6 many species of Flax (*Linum perenne* and *Austriacum*) open. Between 6 and 7, Willow-herbs (*Epilobium angustifolium* and *collinum*), between 7 and 8, *Convolvulus arvensis* and *tricolor*. Between 8 and 9, many Gentians, Speedwells, and Wood-sorrels, and the frequently-cultivated Himalayan Cinquefoil (*Potentilla atrosanguinea*). Between 9 and 10 most Tulips and Opuntias open; between 10 and 11, the Centaury (*Erythrœa*) and Chaffweed (*Centunculus*). Between 11 and 12, *Potentilla recta*. From noon till evening comes a long interval. No plant is known in our latitude which, under ordinary circumstances, opens during the afternoon. Towards sunset, however, it recommences. About 6 p.m. the Honeysuckle opens, shortly followed by the Evening Primrose and Campion. Between 7 and 8 p.m. *Hesperis matronalis* and *tristis*, the Marvel of Peru (*Mirabilis Jalapa*), a few Catchflies (*Silene noctiflora* and *vespertina*) and several Thorn-apples (*Datura Stramonium*). Between 8 and 9 more Catchflies (*Silene longiflora*, *Saxifraga*, *Vallesia*), a Woodruff (*Asperula glomerata*), and a species of Tobacco (*Nicotiana affinis*). Between 9 and 10, the Queen of the Night (*Cereus nycticalus*, represented on Plate VII. opposite page 642, vol. i.) opens.

As it is with the commencement, so is it with the end of flowering; each happens at a definite time, and every flower endures for a determinate period. Flowers which are only open for a single day are termed *ephemeral* flowers. The annexed table shows the hours of opening and closing of a series of ephemeral flowers.

NAME OF PLANT.	OPENS AT	CLOSES AT	NAME OF PLANT.	OPENS AT	CLOSES AT
<i>Allionia violacea</i> .....	3-4 A.M.	11-12 A.M.	<i>Portulaca grandiflora</i> ....	8-9 A.M.	6-7 P.M.
<i>Roemeria violacea</i> .....	4-5 "	10-11 "	<i>Calandrinia compressa</i> ...	9-10 "	1-2 "
<i>Cistus Creticus</i> .....	5-6 "	5-6 P.M.	<i>Drosera longifolia</i> .....	9-10 "	2-3 "
<i>Tradescantia Virginica</i> ..	5-6 "	4-5 "	<i>Arenaria rubra</i> .....	10-11 "	3-4 "
<i>Iris arenaria</i> .....	6-7 "	3-4 "	<i>Portulaca oleracea</i> .....	10-11 "	3-4 "
<i>Hemerocallis fulva</i> .....	6-7 "	8-9 "	<i>Spergula arvensis</i> .....	10-11 "	3-4 "
<i>Convolvulus tricolor</i> .....	7-8 "	5-6 "	<i>Sisyrinchium anceps</i> .....	11-12 "	4-5 "
<i>Oxalis stricta</i> .....	8-9 "	3-4 "	<i>Mirabilis longiflora</i> .....	7-8 P.M.	2-3 A.M.
<i>Hibiscus Trionum</i> .....	8-9 "	11-12 A.M.	<i>Cereus grandiflorus</i> .....	8-9 "	2-3 "
<i>Erodium Cicutarium</i> .....	8-9 "	4-5 P.M.	<i>Cereus nycticalus</i> .....	9-10 "	2-3 "

The number of hours during which these flowers remain open are as follows:—

	Hours.		Hours.		Hours.
<i>Hibiscus Trionum</i> .....	3	<i>Sisyrinchium anceps</i> .....	5	<i>Iris arenaria</i> .....	9
<i>Calandrinia compressa</i> .....	4	<i>Roemeria violacea</i> .....	6	<i>Convolvulus tricolor</i> .....	10
<i>Portulaca oleracea</i> .....	5	<i>Oxalis stricta</i> .....	7	<i>Tradescantia Virginica</i> ....	10
<i>Drosera longifolia</i> .....	5	<i>Mirabilis longiflora</i> .....	7	<i>Portulaca grandiflora</i> .....	10
<i>Arenaria rubra</i> .....	5	<i>Cereus grandiflorus</i> .....	7	<i>Cistus creticus</i> .....	12
<i>Spergula arvensis</i> .....	5	<i>Allionia violacea</i> .....	8	<i>Hemerocallis fulva</i> .....	14
<i>Cereus nycitcalus</i> .....	5	<i>Erodium Cicutarium</i> .....	8		

From these tables we see that plants with ephemeral flowers may be arranged in two groups; those in which the flowers open between early morning and noon, and those which open at the commencement of twilight or during the night. The latter may be distinguished as “night-flowerers”.

Included with the ephemeral flowers are such as open in the evening between seven and eight o'clock, and remain open the whole night and following morning till past midday, or even till evening. For the most part, these close within twenty-four hours of their opening. To these belong several species of Thorn-apple and Evening Primrose, *Morina*, the Marvel of Peru, and a few Cactuses (*Datura Metel* and *Stramonium*, *Ænothera biennis* and *grandiflora*, *Morina Persica*, *Mirabilis Jalapa*, *Echinocactus Tetani*).

Another series of plants have the peculiarity that their flowers open for the first time during the morning, close at evening, and open again the following morning, but fade or fall during the afternoon of the second day. Examples are many: Papaveraceæ, many species of Flax, the Raspberry, a few Cinquefoils and Cactuses (*Glaucium corniculatum* and *luteum*, *Papaver alpinum*, *Linum tenuifolium*, *Rubus Idæus*, *Potentilla recta*, and *Opuntia nana*).

The duration of flowering (i.e. period of persistence of single flowers) in plants which keep open for more than a single day is indicated, for selected examples, in the annexed table:—

2 DAYS.	4 DAYS.	<i>Lilium album.</i>
<i>Centunculus minimus.</i>	<i>Lychnis diurna.</i>	<i>Oxalis lasiandra.</i>
<i>Dianthus prolifer.</i>	<i>Sagina saxatilis.</i>	
<i>Epilobium collinum.</i>	<i>Sedum atratum.</i>	7 DAYS.
<i>Geranium pratense.</i>	<i>Scilla liliohyacinthus.</i>	<i>Ranunculus acer</i> , &c.
<i>Papaver somniferum.</i>	<i>Telephium Imperati.</i>	<i>Pelargonium zonale</i> , &c.
<i>Potentilla atrosanguinea</i> , &c.	<i>Sanguinaria Canadensis.</i>	
<i>Rosa arvensis</i> , &c.		8 DAYS.
<i>Saponaria Vaccaria.</i>	5 DAYS.	<i>Eranthis hiemalis.</i>
<i>Sinapis arvensis.</i>	<i>Eschscholtzia Californica.</i>	<i>Hepatica triloba.</i>
<i>Veronica aphylla</i> , &c.	<i>Fritillaria meleagris.</i>	<i>Parnassia palustris.</i>
	<i>Scilla Sibirica.</i>	<i>Saxifraga bryoides.</i>
3 DAYS.	<i>Erythraea Centaurium.</i>	
<i>Lonicera Caprifolium.</i>	<i>Linum viscosum.</i>	10 DAYS.
<i>Potentilla formosa.</i>		<i>Cyclamen Europæum.</i>
<i>Agrimonia Eupatorium.</i>	6 DAYS.	
<i>Aphyllanthes monspeliensis.</i>	<i>Digitalis purpurea.</i>	12 DAYS.
<i>Galium infestum</i> , &c.	<i>Erythraea pulchella.</i>	<i>Crocus sativus.</i>
<i>Helianthemum alpestre</i> , &c.	<i>Hemerocallis flava.</i>	<i>Saxifraga Burseriana.</i>



18 DAYS.	40 DAYS.	60 DAYS.
<i>Vaccinium Oxyccocos.</i>	<i>Cypripedium insigne.</i>	<i>Oncidium cruentum.</i>
	<i>Odontoglossum (many).</i>	70 DAYS.
30 DAYS.	50 DAYS.	<i>Cypripedium villosum.</i>
<i>Cattleya labiata.</i>	<i>Epidendrum Lindleyanum.</i>	80 DAYS.
<i>Vanda cœrulea.</i>	<i>Phalænopsis grandiflora.</i>	<i>Odontoglossum Rossi.</i>

The duration of flowers varies then, in different species, from three hours to eighty days. These remarkable differences are connected with the amount of pollen produced in the flowers, and with the number of flowers on each plant. They also depend on whether or no the stigma is entirely dependent on insects for pollen. Flowers with numerous stamens and ample pollen, as for instance, Poppies, Cistuses and Portulacas, have but a brief duration, whilst on the other hand, such as have but a single stamen, *e.g.* most Orchids, remain fresh often for weeks. In plants which produce but a single flower throughout the year, as the Snowdrop, the one-flowered Winter-green (*Pyrola uniflora*), Herb Paris and *Trillium*, or at most two or three, as in the Lady's Slipper Orchid (*Cypripedium Calceolus*), and in tropical Orchids of the genera *Oncidium*, *Stanhopea*, and *Cattleya*, the flowers persist fresh and open for long periods. It may happen also that in consequence of unfavourable climatic conditions flowers may be deprived of insect-visits for many days at a time. In the case of flowers so constituted that in the absence of insects no production of seeds is possible, it follows that in some years the whole object of flowering (where but a single or very few flowers are produced) will be jeopardized. It is obviously of advantage to flowers of this kind that they should be able to hold out for a considerable period. The longer they persist the better is their chance of being visited by insects bringing pollen from other plants.

Let us now take the other extreme, a plant producing numerous flowers, one after the other, in the course of a year, flowers which are able in the absence of insects to pollinate themselves. Here the duration of each flower need be only very short. Notwithstanding the short duration of the flowers the plant remains in blossom for weeks or months. The Spiderworts (*Tradescantia crassula*, *Virginica*, &c.) have ephemeral flowers, but they go on producing them for eight weeks, during the whole of which time the plants are daily provided with new ones. The same holds good in most Crucifers, Cistuses, Rock-roses (*Helianthemum*), Droseras, &c. The last-mentioned open their flowers only under very favourable conditions of weather, and then only every other day. At any rate, for *Drosera longifolia* it has been shown that, even in the finest weather, a flower-bud opens on alternate days only. Thus we see that pretty much the same result is accomplished in the two classes; in those plants possessing numerous, ephemeral flowers, and in those with solitary, long-persisting ones.

It has already been explained (p. 107) that in localities where a heavy precipitation of dew obtains, flowers which remain open for long periods are liable to a saturation of their pollen during the night, and that many protective arrangements prevail to minimize this danger. One of the most commonly occurring of these

contrivances is the closing of the flowers at night. The petals fold inwards and become furled in the same positions as they occupied in the bud. Indeed, one may say that the flower becomes a bud again. When consistent with the advantages accruing from insect-visits, flowers close in the evening and only open again next day when the danger of wetting by dew is past. In a great number of cases this periodic opening occurs at the same hour as that at which the flower-bud originally opened. Many flowers open but once again, others twice, thrice, or four times on successive days—the Meadow Saffron daily for twelve days. As soon as any particular kind of insect begins to swarm, those flowers, whose structure is adapted to visits from the variety of insect in question, open. Similarly, when the insects retire to rest, the flowers close lest the pollen be exposed to needless danger. In other words, the flowers of many plants *open and close periodically*.

This remarkable phenomenon has for a long time attracted the attention of Botanists, and Linnæus devised his so-called Floral Clock on the basis of his long-continued observations at Upsala. In this he grouped together plants according to the hours at which they opened and closed their flowers, and ascertained, for every hour of the day, what species were doing either the one or the other. Not only were simple, isolated flowers laid under contribution for this purpose, but the complex heads (capitula) of Composites also, since these periodic movements are very conspicuous in them. True, in Composites it is not the petals of a flower which open and shut, but the flowers (florets) of a head; still the cause and effect are here identical with those in ordinary flowers, and Composites were rightly included in the Floral Clock. If the plants which open and close their flowers periodically be cultivated apart, it is possible to determine the time of day by careful observation in this part of the garden. Formerly, the attempt was often made in Botanic Gardens to construct such a Floral Clock, but never with success, because the plants enumerated by Linnæus do not all flower at the same season. Later, when other fields of Botanical activity came into vogue, it was abandoned as a children's game. Consequently the Floral Clock of Linnæus has fallen into oblivion, and the younger generation of Botanists hardly knows its name. For my own part, I am inclined to give this Clock some consideration, as it has a bearing on several important questions in the life of plants. To recall it to memory, it is annexed below in the table which follows. It was constructed for Upsala, 60° north lat.

3-5 A.M.	5-6 A.M.	7 A.M.
<i>Tragopogon pratense</i> .....open.	<i>Crepis alpina</i> .....open.	<i>Anthericum ramosum</i> .....open.
	<i>Rhagadiolus edulis</i> ..... "	<i>Calendula pluvialis</i> ..... "
	<i>Taraxacum officinale</i> ..... "	<i>Lactuca sativa</i> ..... "
4-5 A.M.	6 A.M.	<i>Leontodon hastile</i> ..... "
<i>Cichorium Intybus</i> ..... "	<i>Hieracium umbellatum</i> ..... "	<i>Nymphæa alba</i> ..... "
<i>Leontodon tuberosum</i> ..... "	<i>Hypocheris maculata</i> ..... "	<i>Sonchus Lapponicus</i> ..... "
<i>Picris hieracioides</i> ..... "	6-7 A.M.	
	<i>Alyssum utriculatum</i> ..... "	7-8 A.M.
5 A.M.	<i>Crepis rubra</i> ..... "	<i>Mesembryanthemum barbatum</i> ..
<i>Hemerocallis fulva</i> ..... "	<i>Hieracium murorum</i> ..... "	<i>Mesembryanthemum lingui-</i>
<i>Papaver nudicaule</i> ..... "	<i>Hieracium Pilosella</i> ..... "	<i>forme</i> ..... "
<i>Sonchus oleraceus</i> ..... "	<i>Sonchus arvensis</i> ..... "	

8 A.M.	11-12 A.M.	3-4 P.M.
<i>Anagallis arvensis</i> .....open.	<i>Sonchus oleraceus</i> ..... shut.	<i>Anthericum ramosum</i> ..... shut.
<i>Dianthus prolifer</i> ..... "	NOON.	<i>Calendula pluvialis</i> ..... "
<i>Hieracium Auricula</i> ..... "	<i>Calendula arvensis</i> ..... "	<i>Hieracium Pilosella</i> ..... "
8-10 A.M.	<i>Sonchus Lapponicus</i> ..... "	4 P.M.
<i>Taraxacum officinale</i> ..... shut.	1 P.M.	<i>Alyssum utriculatum</i> ..... "
9 A.M.	<i>Dianthus prolifer</i> ..... "	4-5 P.M.
<i>Calendula arvensis</i> .....open.	<i>Hieracium chondrilloides</i> ... "	<i>Hypochaeris maculata</i> ..... "
<i>Hieracium chondrilloides</i> ... "	1-2 P.M.	5 P.M.
9-10 A.M.	<i>Crepis rubra</i> ..... "	<i>Hieracium umbellatum</i> ..... "
<i>Arenaria rubra</i> ..... "	2 P.M.	<i>Nyctago hortensis</i> .....open.
<i>Mesembryanthemum crystal-</i>	<i>Hieracium Auricula</i> ..... "	<i>Nymphaea alba</i> ..... shut.
<i>linum</i> ..... "	<i>Hieracium murorum</i> ..... "	6 P.M.
<i>Tragopogon pratense</i> ..... shut.	<i>Mesembryanthemum barbatum</i> .. "	<i>Geranium triste</i> .....open.
10 A.M.	2-3 P.M.	7 P.M.
<i>Cichorium Intybus</i> ..... "	<i>Arenaria rubra</i> ..... "	<i>Papaver nudicaule</i> ..... shut.
<i>Lactuca sativa</i> ..... "	2-4 P.M.	7-8 P.M.
<i>Rhagadiolus edulis</i> ..... "	<i>Mesembryanthemum crystal-</i>	<i>Hemerocallis fulva</i> ..... "
<i>Sonchus arvensis</i> ..... "	<i>linum</i> ..... "	9-10 P.M.
10-11 A.M.	3 P.M.	<i>Cactus grandiflorus</i> .....open.
<i>Mesembryanthemum nodi-</i>	<i>Leontodon hostile</i> ..... "	<i>Silene noctiflora</i> ..... "
<i>florum</i> .....open.	<i>Mesembryanthemum lingui-</i>	MIDNIGHT.
11 A.M.	<i>forme</i> ..... "	<i>Cactus grandiflorus</i> ..... shut.
<i>Crepis alpina</i> ..... shut.	<i>Mesembryanthemum nodiflo-</i>	
	<i>rum</i> ..... "	

To the above clock, adapted to the latitude of Upsala, I append a second, based on long-continued observations at Innsbruck (47° north lat.), 13° south of Upsala.

4-5 A.M.	7-8 A.M.	
<i>Rosa arvensis</i> (June).....open.	<i>Campanula Trachelium</i> (July) op'n	<i>Isopyrum thalictroides</i> (April) op'n
5-6 A.M.	<i>Carlina acaulis</i> (August)... "	<i>Lactuca sativa</i> (Aug.)..... "
<i>Rosa rubiginosa</i> (June)..... "	<i>Carlina vulgaris</i> (August)... "	<i>Lactuca Scariola</i> (Sept.).... "
<i>Solanum nigrum</i> (July)..... "	<i>Crepis rubra</i> (August)..... "	<i>Mamillaria glochidiata</i> (Aug.).. "
6-7 A.M.	<i>Gentiana acaulis</i> (May).... "	<i>Nymphaea alba</i> (Aug.)..... "
<i>Anolla hastata</i> (July)..... "	<i>Geranium lucidum</i> (July)... "	<i>Ornithogalum Narbonense</i>
<i>Cichorium Intybus</i> (July)... "	<i>Gilea tricolor</i> (July)..... "	(July)..... "
<i>Crepis pulchra</i> (July)..... "	<i>Hedynois tubiformis</i> (July) "	<i>Oxalis lasiandra</i> (Aug.)..... "
<i>Dianthus neglectus</i> (July)... "	<i>Hieracium Pilosella</i> (July).. "	<i>Veronica Persica</i> (June).... "
<i>Gallasia villosa</i> (July)..... "	<i>Hypecoum grandiflorum</i> (July).. "	9-10 A.M.
<i>Hieracium amplexicaule</i>	<i>Hypochaeris maculata</i> (June) "	<i>Anagallis arvensis</i> (July)... "
(July)..... "	<i>Lactuca muralis</i> (July)..... "	<i>Anemone Hepatica</i> (April).. "
<i>Hieracium aurantiacum</i>	<i>Oxalis Valdiviana</i> (July)... "	<i>Anemone nemorosa</i> (April).. "
(July)..... "	<i>Sonchus arvensis</i> (August).. "	<i>Calendula officinalis</i> (Sept.) "
<i>Lactuca perennis</i> (August).. "	<i>Specularia Speculum</i> (July) "	<i>Colchicum autumnale</i> (Sept.) "
<i>Lampsana communis</i> (July) "	<i>Tolpis barbata</i> (August).... "	<i>Crepis pulchra</i> (July)..... shut.
<i>Linum grandiflorum</i> (July) "	8-9 A.M.	<i>Crocus aureus</i> (March)..... open.
<i>Linum viscosum</i> (July)..... "	<i>Adonis vernalis</i> (April)..... "	<i>Draba verna</i> (March)..... "
<i>Mulgedium Plumieri</i> (July) "	<i>Brassica oleracea</i> (Sept.).... "	<i>Eranthis hiemalis</i> (March).. "
<i>Ranunculus acer</i> (July)..... "	<i>Diplotaxis tenuifolia</i> (Sept.) "	<i>Eschscholtzia Californica</i>
<i>Solanum tuberosum</i> (July).. "	<i>Gentiana asclepiadea</i> (Aug.) "	(June)..... "
<i>Sonchus oleraceus</i> (June) ... "	<i>Gentiana cruciata</i> (July)... "	<i>Gallasia villosa</i> (July)..... shut.
<i>Taraxacum officinale</i> (June) "	<i>Gentiana utriculosa</i> (June). "	<i>Oxalis Acetosella</i> (April).... open.
<i>Tragopogon floccosus</i> (July) "	<i>Geranium columbinum</i> (Aug.).. "	<i>Tulipa sylvestris</i> (May)..... "
<i>Tragopogon orientalis</i> (July) "	<i>Helianthemum alpestre</i> (June).. "	<i>Tussilago Farfara</i> (April).. "
		<i>Veronica Chamædrys</i> (May) "



10-11 A.M.	<i>Eschscholtzia Californica</i> (July) ..... shut.	<i>Gentiana asclepiadea</i> (Aug.) shut
<i>Abutilon Avicennæ</i> (July)... open.	<i>Gentiana utriculosa</i> (July).. „	<i>Lactuca perennis</i> (Aug.).... „
<i>Anemone Pulsatilla</i> (March) „	<i>Helianthemum alpestre</i> (June) „	<i>Oxalis Acetosella</i> (April) ... „
<i>Anemone vernalis</i> (March).. „	<i>Hieracium aurantiacum</i> (July) ..... „	<i>Sternbergia lutea</i> (Oct.)..... „
<i>Centunculus minimus</i> (Aug.) „	<i>Hypecoum grandiflorum</i> (July) ..... „	<i>Tulipa sylvestris</i> (May)..... „
<i>Erythræa pulchella</i> (Aug.).. „	<i>Lactuca Scariola</i> (Sept.) ... „	<i>Tussilago Farfara</i> (April).. „
<i>Lampsana communis</i> (July) shut.	<i>Nicandra physaloides</i> (July) „	<i>Veronica Chamædrys</i> (May) „
<i>Tragopogon floccosus</i> (July) „	<i>Ornithogalum Narbonense</i> (July) ..... „	<i>Veronica Persica</i> (June).... „
<i>Tragopogon orientalis</i> (July) „	<i>Oxalis Valdiviana</i> (July)... „	6-7 P.M.
11-12 A.M.	<i>Specularia Speculum</i> (July) „	<i>Anoda hastata</i> (July)..... „
<i>Crocus lævigatus</i> (Oct.)..... open.	4-5 P.M.	<i>Campanula Trachelium</i> (July),,
<i>Hieracium amplexicaule</i> (July) ..... shut.	<i>Calendula officinalis</i> (Sept.) „	<i>Carlina acaulis</i> (Aug.)..... „
<i>Mesembryanthemum crystal- linum</i> (July) ..... open.	<i>Centunculus minimus</i> (Aug.) „	<i>Crepis rubra</i> (July)..... „
<i>Nicandra physaloides</i> (July) „	<i>Crocus aureus</i> (March) ..... „	<i>Dianthus neglectus</i> (July)... „
<i>Sternbergia lutea</i> (Oct.)..... „	<i>Crocus lævigatus</i> (Oct.)..... „	<i>Eranthis hiemalis</i> (March).. „
12-1 P.M.	<i>Diploxaxis tenuifolia</i> (Sept.) „	<i>Gentiana acaulis</i> (May).... „
<i>Sonchus arvensis</i> (Aug.)..... shut.	<i>Geranium columbinum</i> (Aug.) „	<i>Hypochæris maculata</i> (June) „
1-2 P.M.	<i>Isopyrum thalictroides</i> (April) „	<i>Silene Saxifraga</i> (July).... open.
<i>Hieracium Pilosella</i> (July). „	<i>Linum grandiflorum</i> (July) „	7-8 P.M.
<i>Lactuca sativa</i> (Aug.)..... „	<i>Linum viscosum</i> (June)..... „	<i>Carlina vulgaris</i> (Aug.).... shut.
<i>Sonchus oleraceus</i> (July).... „	<i>Mesembryanthemum crystal- linum</i> (July) ..... „	<i>Gentiana cruciata</i> (July)... „
2-3 P.M.	<i>Oxalis lasiandra</i> (June).... „	<i>Geranium lucidum</i> (July)... „
<i>Cichorium Intybus</i> (Aug.)... „	5-6 P.M.	<i>Gileæ tricolor</i> (July) ..... „
<i>Hedypnois tubiformis</i> (July) „	<i>Abutilon Avicennæ</i> (July)... „	<i>Nymphæa alba</i> (Aug.) ..... „
<i>Lactuca muralis</i> (July)..... „	<i>Adonis vernalis</i> (April)..... „	<i>Ranunculus acer</i> (June).... „
<i>Mamillariaglochidiata</i> (Aug.),,	<i>Anemone Hepatica</i> (April).. „	<i>Silene Vallesia</i> (July)..... open.
<i>Solanum tuberosum</i> (July).. „	<i>Anemone nemorosa</i> (April).. „	<i>Tolpis barbata</i> (Aug.)..... shut.
<i>Taraxacum officinale</i> (June) „	<i>Anemone Pulsatilla</i> (March) „	8-9 P.M.
3-4 P.M.	<i>Anemone vernalis</i> (March).. „	<i>Brassica oleracea</i> (Sept.).... „
<i>Anagallis phænicea</i> (July).. „	<i>Colchicum autumnale</i> (Sept.) „	<i>Mulgedium Plumieri</i> (July) „
<i>Erythræa pulchella</i> (Aug.).. „	<i>Draba verna</i> (March) ..... „	<i>Rosa arvensis</i> (June) ..... „
		<i>Rosa rubiginosa</i> (June)..... „
		<i>Silene nutans</i> (June)..... open.
		<i>Solanum nigrum</i> (Sept.).... shut.

In the tables below are collated a few species whose times of opening and closing have been recorded for both Upsala and Innsbruck.

## OPENING OF FLOWERS AT UPSALA AND INNSBRUCK.

NAME OF PLANT.	AT UPSALA.	AT INNSBRUCK.	DIFFERENCE IN HOURS.
<i>Cichorium Intybus</i> .....	4- 5 A.M.	6- 7 A.M.	2
<i>Hemerocallis fulva</i> .....	5 „	6- 7 „	1-2
<i>Sonchus oleraceus</i> ....	5 „	6- 7 „	1-2
<i>Taraxacum officinale</i> .....	5- 6 „	6- 7 „	1
<i>Hypochæris maculata</i> .....	6 „	7- 8 „	1-2
<i>Sonchus arvensis</i> .....	6- 7 „	7- 8 „	1
<i>Lactuca sativa</i> .....	7 „	8- 9 „	1-2
<i>Nymphæa alba</i> .....	7 „	8- 9 „	1-2
<i>Anagallis arvensis</i> .....	8 „	9-10 „	1-2
<i>Arenaria rubra</i> .....	9-10 „	10-11 „	1

## CLOSING OF FLOWERS AT UPSALA AND INNSBRUCK.

NAME OF PLANT.	AT UPSALA.	AT INNSBRUCK.	DIFFERENCE IN HOURS.
<i>Taraxacum officinale</i> .....	8-10 A.M.	2-3 P.M.	5-6
<i>Cichorium Intybus</i> .....	10 "	2-3 "	4-5
<i>Lactuca sativa</i> .....	10 "	1-2 "	3-4
<i>Sonchus arvensis</i> .....	10 "	12-1 "	2-3
<i>Sonchus oleraceus</i> .....	11-12 "	1-2 "	2
<i>Arenaria rubra</i> .....	1- 3 P.M.	3-4 "	1
<i>Hypochaeris maculata</i> .....	4- 5 "	6-7 "	2
<i>Hemerocallis fulva</i> .....	7- 8 "	8-9 "	1
<i>Nymphaea alba</i> .....	5 "	7-8 "	2-3

From a perusal of these tables it appears that flowers both open and close earlier in the day at Upsala than at the more southerly situated Innsbruck. This result, especially the earlier opening, is probably connected with the fact that the sun during the flowering-season of the plants in question rises about an hour and a half earlier at Upsala than at Innsbruck.

With this difference in time of opening of flowers, the results of observations carried out in mountainous districts on plants which extend from the low warm valleys up into the hills entirely harmonize. The Hepatica (*Anemone Hepatica*) blooms on the valley-floor at Innsbruck (560 metres) in March, at a time when the sun rises at 6 a.m., its flowers opening each day between 9 and 10 a.m. In the mountain glens, south of Innsbruck, at a height of 1560 metres above the sea-level, it blossoms in May, at a time when the sun rises at 5 a.m. Here its flowers open between 8 and 9 a.m. *Lampsana communis* and *Sonchus arvensis* blossom in July in the meadows of the Innthal (560 metres); in the adjacent Gschnitzthal (660 metres higher) in August. The sun rises at Innsbruck in July at 4.30, and the capitula of these two plants open in the Innthal between 6 and 7 a.m.; in August the sun rises about an hour later, and the same plants open correspondingly in the highly-situated Gschnitzthal also an hour later, *i.e.* between 7 and 8 a.m.

Several ornamental garden plants are indefatigable in their blossoming. For months on end flowers upon flowers are produced, only ceasing with the on-coming of winter. As an example *Catananche cœrulea* may be instanced; at Vienna it remains in flower from the end of June till the end of October. Its capitula show a periodic opening and closing, but they differ in the hour at which they execute their movements according to the season. At the end of June and beginning of July they open between 4 and 5 a.m., in August and in the first half of September between 5 and 6, whilst in the latter part of September and beginning of October they open between 6 and 7 a.m. Finally, in the widely-distributed Dandelion (*Taraxacum officinale*), to be met with in isolated examples flowering in spring, summer, and autumn, the same thing may be observed. In May it opens between 7 and 8, at midsummer between 6 and 7, in August between 7 and 8, and in September between 8 and 9 a.m.

The times of opening and closing given here and in the Floral Clock apply only to fine days. In cloudy, misty, and rainy weather, the flowers remain closed or only partly open; or, when these conditions are but temporary, a conspicuous retardation of opening and closing takes place, which cannot, however, be indicated numerically. Further, the observations given above relate in particular to plants well placed in regard to illumination. Such a limitation of the flowers under observation is absolutely essential, if tolerably reliable results are required. The greatest care is necessary, especially in the case of flowers which open quickly. Thus one finds with the almost suddenly-opening Gentians (*Gentiana ciliata*, *Bavarica*, and *verna*), that whilst those growing on the east or south side of a hillock have already opened wide their flowers, those a few yards away with a northerly aspect still keep their flowers closed. On luxuriant *Opuntia*-plants it is quite common for the flowers on the branches of the sunny side to open a long time before those on the shady side, and this with flowers of the same age.

The whole of these observations point to the fact that the opening of flowers is especially promoted by sunshine. Exactly how it is brought about, how the influence of the sun's rays in these opening-movements of flowers affects the tension of the tissues, is by no means easy of explanation. Still the question is so full of interest that it is well worth our consideration. First, we may inquire whether it is light or heat which gives the impulse to the remarkable changes in tension which lead to the movements of the petals. Plants were employed, for the solution of this question, whose flowers open directly they are reached by the first morning rays of sunshine. Specimens of *Gentiana Rhetica* and *asclepiadea* were placed in a roomy cylinder of glass in which the temperature was maintained at a low and uniform temperature. This was effected by surrounding the cylinder by a second, larger one, and causing a stream of water of a constant temperature of 7° C. to circulate in the space between the cylinders. Since this mantle of water only permitted rays of light and not of heat to pass, it would be due solely to the action of the former if the flowers under experiment opened. As the rays of the morning sun reached the cylinder the Gentians within opened their flowers. In view of this result one is justified in assuming that the opening is occasioned by the rays of light. But that it arises solely from this cause were too hasty a conclusion, as appears from the following control-experiment, conducted upon the same Gentians. They were, whilst closed, placed in a dark room over the still hot iron of a stove in a situation where the thermometer indicated 42° C. Within 3 minutes they had all completely opened.

This apparent contradiction may be explained by the assumption that the rays of light which fell upon the closed Gentian flowers in the cylinder were converted into heat. As we know, if rays of light strike any object and are not entirely reflected from its surface, they warm it (*cf.* vol. i. p. 519). This probably is the case with the Gentians, and the phenomenon may be explained as follows. The light-vibrations are communicated to the flowers and converted into vibrations of heat. This heat produces changes in the turgidity of the tissues, affecting their tension



and growth. The active energy of the heat is converted into another form of movement which ultimately alters the position of the petals, and we see the flowers opening. This explanation, further, harmonizes with the ascertained fact that under the influence of light and warmth the watery contents of certain cells in dead tissues undergo a rapid alteration, and that even in portions of flowers whose cells contain no living protoplasm changes in tension are brought about. It also agrees with the conception that the periodic opening and closing of flowers stands in relation to those chemical changes and molecular re-arrangements which we know as Respiration, Metabolism, and Growth. It has been demonstrated that flowers which exhibit periodic movements do not cease their growth on their first opening, but continue to stretch both in length and breadth. The perianth-leaves of Winter Aconites (*cf.* p. 114), Meadow Saffrons, Anemones, and Gentians, and the ligulate florets of the capitula of the Daisy, Marigold, and Leopard's Bane grow in length considerably every night. Only so long as this growth continues is an opening or closing possible, these movements cease simultaneously with growth.

The suggestion already offered as to the significance of anthocyanin (vol. i. p. 520) agrees with the idea that light is converted into heat in the tissue of the sepals. It was made probable, in the page cited, that the variously-coloured pigments known as anthocyanin possessed amongst other properties that of converting light into heat. It is particularly interesting to note that the white sepals of periodically opening and closing Anemones (*Anemone alpina*, *baldensis*, *nemorosa*, *sylvestris*, *trifolia*, &c.), show a red, violet, or blue tinge on the under side. Quite similarly coloured are the ligulate florets of many Composites (e.g. *Anacyclus officinarum*, *Bellis perennis*, *Calendula pluvialis*, *Hieracium Pilosella*). It is of course the under-surfaces of the sepals, petals and marginal florets of closed flowers and capitula which are alone visible. When they are closed they appear red, violet, or blue; when open, white (yellow in *Hieracium Pilosella*). The first rays of the morning sun fall first on the layers of cells coloured by anthocyanin, and we readily understand what an important part this substance may play in converting the light into heat.

Seeing that the opening of flowers and flower-buds stands to the rays of the morning sun in the relation of effect to cause, we may infer that the shutting at evening is connected with the waning light and heat. It is also to be expected that closed flowers may be made to open at will by appropriate illumination and warmth, and conversely. This at any rate holds good for a number of plants. It has been already remarked of *Gentiana nivalis* (*cf.* p. 116) that in the course of an hour, when the sun alternately shines and is obscured by clouds, it will repeatedly open and close. This is also the case with several other Gentians, with Tulips, Meadow Saffrons, and a Flax (*Linum catharticum*). In them, also, is the effect of earlier rising and later setting of the sun in northern latitudes especially conspicuous. But in the majority of flowers with periodic opening and closing, the matter is not quite so simple. True, the majority of species of Flax and Wood-sorrel, and the marginal florets of Composite heads respond to illumination and

warmth by movements, as when the sun's rays reach them in the morning after the night's rest. But when, subsequently, they have once closed it is impossible to make them open again completely the same day, vary the illumination as you will. Indeed, in the majority of these flowers the closing occurs not towards sunset, but at high noon; thus the heads of *Lampsana* and *Tragopogon* shut before the sun reaches the zenith, and several hours before the maximum temperature is attained. Then, again, there are the Dame's Violet (*Hesperis matronalis*), and many Caryophyllaceæ, which only begin to open their flowers as light and temperature wane, and shut them again ere the sun has risen. To explain these movements as being a direct consequence of illumination and warmth were as futile as to explain the sleep of man and other animals as the immediate consequence of on-coming night. Undeniably there is an indirect connection with the change from light to darkness, from warmth to cold, but conceivable only in the same manner as assimilation, metabolism and growth, in plants and animals, observe the periodicity of day and night. We may state it in this way: in different organisms certain resultant effects of assimilation, metabolism and growth become manifest at different times, the particular time depending on the advantages accruing to the organism in its special circumstances. For Man the night is the most advantageous time for sleep; for Owlet Moths and other Noctuæ it is not. For *Lampsana communis* it is of advantage in respect of its ultimate self-fertilization (to be described hereafter) that its capitula should close before noon, for the Dame's Violet and numerous Catchflies (*Silene*), that their flowers should open in the evening to receive visits from Moths (*cf.* p. 154).

These observations offer no complete or satisfactory explanation. It still remains unsolved how, in so many plants, periodic movements not depending directly upon change in the environment have become hereditary. For those who are satisfied with a fine-sounding Greek or Latin word in place of an explanation, it may be remarked that these movements of floral leaves just described have been termed *Autonomous movements*.

#### RECEPTION OF FLOWER-SEEKING ANIMALS AT THE ENTRANCE TO THE FLOWER.

In a volume written years ago (*Plants and their Unbidden Guests*) I divided the animals which come as guests to partake of the pollen, honey, &c., of flowers into the bidden and unbidden. The former greatly profit the plant by their visits, and there exist a multiplicity of arrangements for attracting them; the latter are unprofitable and, frequently, positively disadvantageous; when they come they must be hindered and sent away. The methods of flowers for attracting bidden guests have been already described, the reception of these and the unbidden ones at the entrance to the flower must now be considered.

And first let us see what are the arrangements which exist to enable the bidden guests to obtain the food they desire without loss of time, exertion, and, most

important of all, with advantage to the plant itself. It were a contradiction for the invited guests on their arrival to find the honey-secreting flower inaccessible, or that a flower should remain widely open when no more nourishment was to be obtained—when the meal, so to speak, was finished.

These obvious truisms apply to flowers still in bud, which it would be premature for insects to visit, and to such as have no further need of insects. It commonly happens that when a flower is pollinated its means of attraction—coloured or scented corolla—disarticulates and falls off. But cases exist in which the petals, having served this purpose, do not at once fall away, but are retained, having another part to play. When this is the case it is undesirable that they should interfere with the other younger flowers by competing with them for visitors; in a word, they must be rendered inaccessible. This is most frequently accomplished by the petals assuming the position they occupied in the bud, and often enough such a flower absolutely resembles a bud, as in the *Yucca*, represented in fig. 240<sup>1</sup>, p. 157. Sometimes a lobe of the perianth or of the sheath-like spathe folds down, obstructing the entrance, as in many Aroids, and, in particular, in the Birthwort (*Aristolochia Clematitis*, cf. fig. 257<sup>8</sup>). In a number of cases the old flowers, which have no further need of insects, bend down out of the way of the younger ones, as may be seen in a number of Papilionaceæ and Boragineæ (cf. vol. i. p. 744). In *Morina Persica* and in the Brazilian Rubiaceæ, *Exostemma longiflorum*, the old flowers not only bend down, but undergo a peculiar change in colour, so that they are no longer noticed by insects. At the time of flowering the tubular corollas of these flowers are white and attractive to night-flying moths, being visible in the dark at some distance; but as soon as they are pollinated the corollas fade and bend down, assuming ere the following night a lurid red tinge, so that they are no longer visible in the dark.

It is similarly capable of easy demonstration that flowers provided with allurements for animals become conspicuous and accessible only at that period when visits are of real advantage. Their accessibility is then promoted as much as possible. In addition to being open the flowers are directed towards the side from which the visits of the most welcome guests are expected. In many plants, of which the Crown Imperial (*Fritillaria*), Foxglove (*Digitalis*), and *Campanula* may serve as types, the at first erect flower-stalks bend down sharply just before the opening of the flowers, so that the entrance is directed towards the ground. This position is inconvenient and unsuited to animals which would suck the honey, hovering over the flowers, to flies, accustomed to lick up honey from a flat surface, to such insects as are too timid to venture into the inside of a hollow flower, finally to beetles which require large amounts of deposited pollen. To bees and humble-bees, however, these flowers are accessible; supported by the projecting stigmas, style, and stamens, or sometimes by hairs, they easily climb up to the honey-secreting dome of the bell. Probably these insects prefer bell-shaped flowers, since here they have no competitors to fear. The ready welcome thus offered to the most industrious of all flower-visitants has this further advantage, that the desired transfer of pollen



from plant to plant is accomplished with certainty and despatch; it may be said of these hanging bell-flowers that they are directed towards the side from which the most welcome of all guests will reach them. Nor must it be forgotten that from this pendent position accrue many other advantages; thus the pollen is well protected from wet by the corolla (*cf.* p. 118), and numerous little Hymenoptera, useful in carrying pollen, use these bells as night-quarters (*cf.* p. 163).

In a large number of plants, though the closed buds are directed upwards, the



Fig. 256.—Preparation of Flowers for Insect-visits in the Laburnum (*Cytisus Laburnum*).

<sup>1</sup> Erect raceme; all the flowers still closed.

<sup>2</sup> Pendent raceme; some of the flowers open.

flower-stalks bend down on opening, so that the entrance to the flower is directed sideways. When, at length, insect-visits are no further required, the older flowers collapse and point downwards. This change in the direction of the flower may be well observed in Honeysuckle (*Lonicera*), Evening Primrose (*Oenothera*), *Acanthus*, in Balsams (*Impatiens*), *Galega*, *Melilotus*, and many of the Clovers (*Trifolium*, *cf.* fig. 252<sup>9</sup> p. 184).

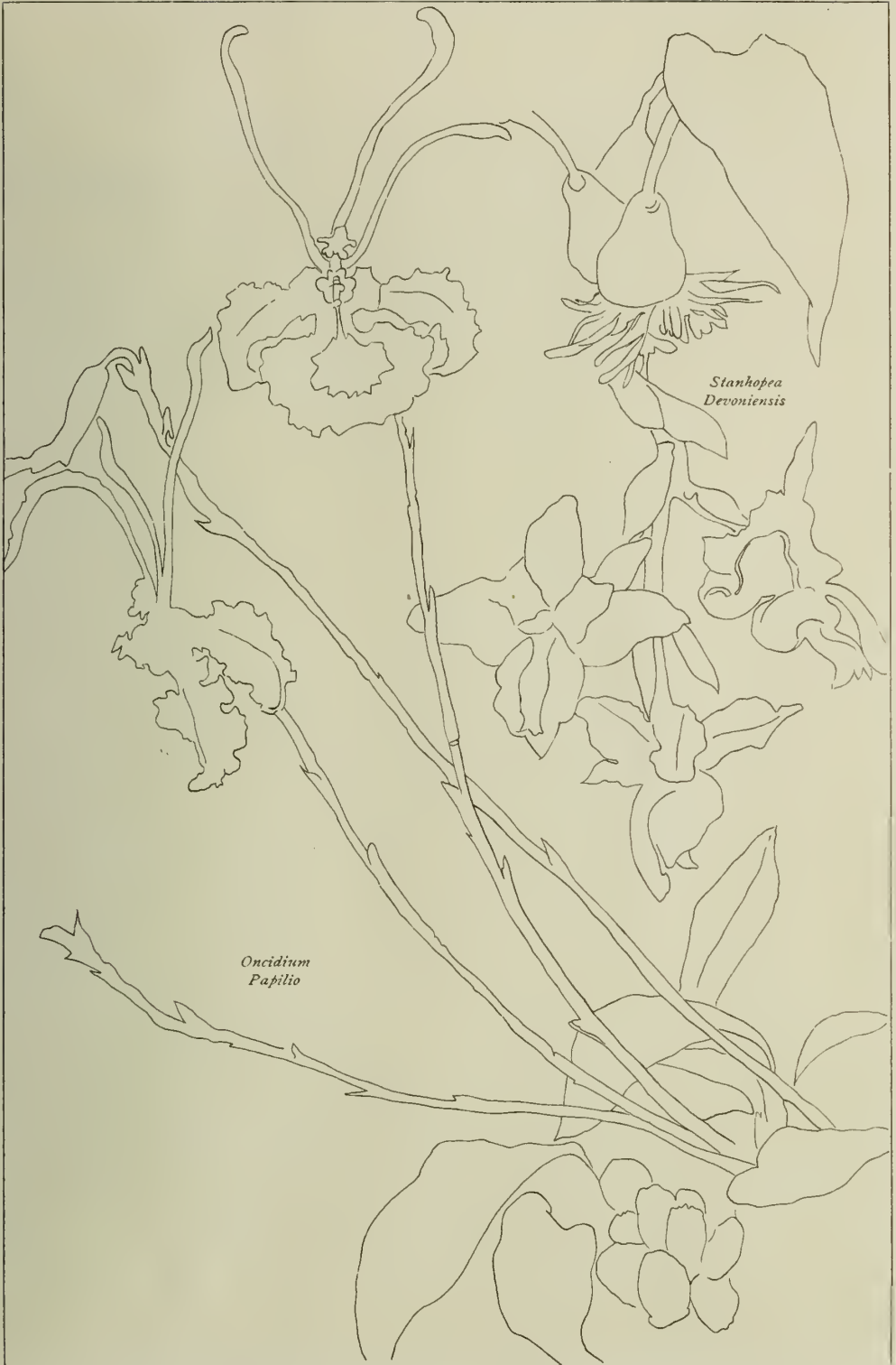
Very peculiar is the behaviour in a number of Papilionaceæ, of which the Laburnum (*Cytisus Laburnum*) may be taken as type (*cf.* fig. 256). The axis of the raceme remains erect so long as all the flowers of the inflorescence are in bud, the individual flowers being so placed that the standard is above and the keel

below (fig. 256<sup>1</sup>); later, the rachis becomes pendent, and the apex of the inflorescence points downwards. The buds are now so placed that the standard is below. Before the standard unfurls and the flowers become accessible, however, the stalk of each flower twists round through nearly 180°, so that the standard is again brought uppermost (cf. fig. 256<sup>2</sup>). In this position the keel is a convenient platform for visiting insects to alight upon. It is of interest to note that if the young racemes are forcibly retained in the erect position by means of strings, the twisting of the flower-stalks does not occur, or only to a very slight extent. In the nearly allied *Laburnum Alschingeri* the racemes are always borne erect, and there is no twisting of the stalks at all; by this character the two species may be readily distinguished.

Many examples of the same phenomenon are furnished by Orchids. Here, however, the twisting is accomplished not by true flower-stalks but by the stalk-like inferior ovaries. In Orchid flowers one member of the perianth, the lip or labellum, is conspicuous by its shape and size, and serves in more than two-thirds of all Orchids as a landing-stage for insects. This petal is directed upwards in the bud, and in a few Orchids always retains this position, as in the vanilla-scented *Nigritella* and in *Epipogium* (cf. fig. 257<sup>10</sup>). But in the majority of Orchids, such, for example, as grow in the meadows with erect spikes of flowers, the ovary undergoes a spiral twisting which brings the lip below so as to serve as a platform for the insects. Nor is this confined to our indigenous Orchids; it occurs also in tropical, epiphytic forms which grow perched on branches of trees or ledges of rock, when they have an upright rachis to the inflorescence; as, for instance, in *Oncidium Papilio*, represented in the accompanying Plate XIII., entitled, "West Indian Orchids". Many of these epiphytic Orchids, however, have not ascending but more or less pendent inflorescences; this is markedly the case in *Stanhopea*, of which a species, *Stanhopea Devoniensis*, is represented in the plate beside the *Oncidium*. Such flowers do not require to twist to bring the lip into the position in question. Indeed, in this and many other similar Orchids no twisting of the ovary takes place. If, however, a young spike of *Stanhopea* be fixed in an erect position, the flowers will all twist within twenty-four hours and take up the position which they would have occupied had the inflorescence been pendulous.

Altogether peculiar is the state of affairs in *Gongora galatea*, a tropical American Orchid sometimes introduced into European hot-houses. As in *Stanhopea*, the spikes are pendulous from the branches of old trees, but the lip of the flower in its original position below is unsuited as a platform for insects. Consequently the ovaries twist through 180°, so that the lip stands above and is of service to visiting insects.

It is an interesting circumstance that all the flowers on many erect, flowering axes turn towards the same side, so that a one-sided spike or raceme results, as in *Vicia*, *Digitalis*, *Corydalis*, and *Penstemon*. The entrance to the flowers is directed towards the side from which the visits of insects or humming-birds may be expected. When, for instance, a Foxglove (*Digitalis*) grows by the edge of a wood,









WEST INDIAN ORCHIDS.





it turns all its flowers away from the shaded side where insects are not abundant, and directs them towards the sunny meadow swarming with bees and humble-bees. Some Labiates belonging to the genera *Salvia* and *Satureja* turn all their flowers one way only when they stand close to a steep wall. When they are equally exposed on all sides their flowers are directed towards all the points of the compass. A similar behaviour is observable in many plants which grow on the narrow mouldings of old, ruined walls, or on the ledges of steep rock faces, as, for instance, in the Snapdragon (*Antirrhinum majus*) and in *Haberlea rhodopensis* of the Balkans; both of these turn their flowers away from the wall or rock, even when these backgrounds are well warmed and lighted by the sun.

The visitors to laterally-directed flowers include Syrphidæ, Owlet-moths, Hawk-moths, Humming-birds—indeed all animals which suck honey whilst hovering in front of the flowers. As they require no platform, we find all flowers of this type destitute of anything of the kind.

Flowers which are visited by sun-birds (Nectariniæ), humming-birds and by night-flying moths are likewise destitute of plates, ridges, fringes, pegs, or knobs on which the animals might alight or cling. The lobes of the corolla which close the flower in bud take, on opening, a position in which they are useless as perches; indeed they bend right back so as to impede the hovering animals as little as possible as they suck up the honey with their probosces or bills. As examples may be mentioned the Honeysuckle (*Lonicera Caprifolium*), the Orchid *Habenaria bifolia* visited by Hawk-moths, and *Melanthus major* sought by small honey-drinking sun-birds (cf. figs. 258<sup>9, 10, 11, 12, 13</sup>). When a well-developed edging or fringe is present in flowers adapted to crepuscular Lepidoptera and Humming-birds, as in *Mirabilis longiflora*, *Nicotiana affinis*, *Posoqueria fragrans*, *Narcissus poeticus*, and *Oenothera biennis*, it serves from its delicacy and position not as a platform, but, in virtue of its conspicuous white or yellow colour, as an attractive organ visible at a considerable distance in the gloaming.

Otherwise is it with flying animals which must first alight on the flower and then penetrate to the concealed honey. Like doves entering a dove-cote, they require a platform, and in point of fact such a provision is found in such laterally-directed flowers as depend on this class of visitor

In *Epipogium aphyllum* the "column" pointing obliquely downwards forms a convenient platform for humble-bees (*Bombus lucorum*, cf. figs. 257<sup>10, 12, 13</sup>). But on the whole the column of Orchid-flowers is rarely used in this way. Very often the stamens or style project well beyond the margin of the flower and serve this purpose, as, for instance, in the Horse Chestnut (*Æsculus*), many Liliaceæ (*Funkia*, *Anthericum*, *Paradisia*, *Phalangium*), Viper's Bugloss (*Echium*), *Dictamnus* and *Pæderota*, similarly in the large-flowered Speedwells (*Veronica*, cf. fig. 257<sup>1</sup>). More frequently, however, the margin of the perianth or corolla is modified for this purpose. Especially noteworthy in this respect are the Aristolochias, on the flowers of which there exists an almost endless series of sometimes flattened, sometimes perch-like, alighting-platforms. In *Aristolochia ringens* (fig. 242, p. 166), it

resembles a sugar-scoop; in the Brazilian *Aristolochia labiosa* (fig. 257<sup>6</sup>), there is a broad heart-shaped expansion in front of the narrow entrance to the flower; in *Aristolochia cordata* (fig. 257<sup>7</sup>) there is an elongated, flagelliform perch for the flies; whilst in our own *Aristolochia Clematitis* (figs. 257<sup>8</sup> and 257<sup>9</sup>) there is a slightly excavated lip on which the midges can alight before entering the flower.

A multifarious variety of arrangements is met with in the perianths of Orchids and in the corollas of bi-labiate flowers for promoting access to the flowers. There



Fig. 257.—Arrangements for the reception of Insects at the entrance to the Flower.

<sup>1</sup> *Veronica Chamædrys*. <sup>2</sup> *Ophrys cornuta*. <sup>3</sup> *Corydalis lutea*, from the front. <sup>4</sup> The same, from the side. <sup>5</sup> *Galeopsis grandiflora*. <sup>6</sup> *Aristolochia labiosa*. <sup>7</sup> *Aristolochia cordata*. <sup>8</sup> *Aristolochia Clematitis*; the lowermost flower is faded and has bent down, its lip is folded over the entrance to the flower. <sup>9</sup> Longitudinal section of a flower of *Aristolochia Clematitis*; within the enlarged cavity of the flower are two midges (*Ceratopogon*) temporarily imprisoned by the reversed hairs of the tube. <sup>10</sup> Flower of *Epipogium aphyllum*. <sup>11</sup> Pollinia of *Epipogium*. <sup>12</sup> Column of *Epipogium* showing the small heart-shaped rostellum. <sup>13</sup> Shows the pollinia of *Epipogium* attached by their sticky rostellum to a pencil, in process of withdrawal. <sup>9</sup>, <sup>11</sup>, <sup>12</sup>, <sup>13</sup> somewhat enlarged; the other figures natural size.

are all sorts of lobings and sinuses, fringes, pegs, and knobs on the lower lip which serve as landing-stages for alighting and as fulcrums for further explorations to numerous flies, wasps, bees, humble-bees, and butterflies. In the noble Orchid *Phalænopsis Schilleriana* (cf. fig. 258<sup>1</sup>) the smooth and complex labellum has a little projection not far from its point of attachment which resembles, and indeed serves, as a footstool to the visiting flies. Behind the footstool is the column, the apex of which is occupied by the anther, and whose lower portion is excavated into



a stigmatic cavity. Leading into the honey-lined stigmatic cavity is a circular aperture or window, and projecting into the upper margin of this window is the little pointed, triangular rostellum like the bill of a bird (fig. 258<sup>2</sup>). When a fly desires to abstract honey from the stigmatic cavity, it stands on the footstool and puts its head in at the window (fig. 258<sup>5</sup>). In doing so it touches the extremely sticky tip of the rostellum, which sticks to the top of its head. When satisfied, the fly, in vacating the footstool, drags the two pollinia (pollen-masses), which

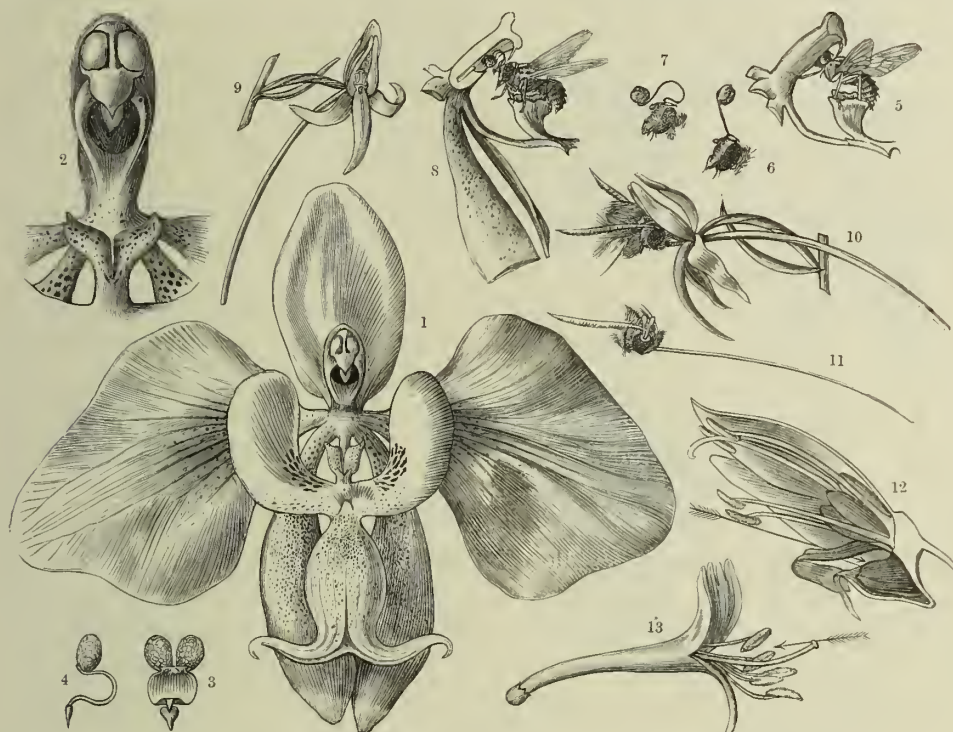


Fig. 258.—Arrangements for the reception of Insects at the entrance to the Flower.

- <sup>1</sup> Flower of *Phalaenopsis Schilleriana*. <sup>2</sup> Column of this *Phalaenopsis*; in front of it is the little bi-lobed footstool. <sup>3</sup> Pollinia of *Phalaenopsis* with heart-shaped gland; seen from in front. <sup>4</sup> The same, seen from the side. <sup>5</sup> A Fly which has alighted upon the footstool is introducing its head into the stigmatic cavity, and simultaneously becoming attached to the gland. <sup>6</sup> Head of the Fly with attached pollinia. <sup>7</sup> The same, the stalk of the pollinia has become bent like a swan's neck. <sup>8</sup> A Fly introducing the pollinia into the stigmatic cavity of another flower; the column is shown in longitudinal section. <sup>9</sup> Flower of *Habenaria bifolia*. <sup>10</sup> The same flower visited by *Sphinx pinastri*; the head of the Sphinx alone is represented, its proboscis has been introduced into the long spur. <sup>11</sup> Head of *Sphinx pinastri* with long proboscis. <sup>12</sup> Flower of *Melianthus major*, seen from the side, after removal of some of the petals. <sup>13</sup> Flower of *Lonicera Etrusca*. <sup>2, 3, 4, 6, 7</sup> slightly enlarged; the other figures natural size.

are attached to the rostellum, out of the anther, and goes away with them on its head (258<sup>6</sup>). It now visits another flower and again alights upon the footstool. Meanwhile the stalk of the two pollinia has bent forwards, like a swan's neck (258<sup>7</sup>), and as the fly puts its head in at the window the pollinia precede it into the stigmatic cavity and remain sticking to the wall (258<sup>8</sup>).

Remarkable, also, is the threshold provided for alighting insects on the lower lip of *Ophrys cornuta* and of the Hemp-nettle (*Galeopsis Tetrahit*). The lip of the



former has two hollow projecting pegs which give the whole flower a horned appearance (fig. 257<sup>2</sup>), that of the latter two pegs, also hollow (fig. 257<sup>5</sup>). In the Snapdragon (*Antirrhinum*) and in the allied Toad-flax (*Linaria*) two remarkable knobs, projecting from the lower lip, serve as a platform for insects which, by exerting pressure, force down the lower lip and gain access to the flower. It is most entertaining to observe how a Humble-bee buzzes about till it alights on the two knobs of the lower lip, and then, having opened the mouth by means of hinges on either side of the corolla, suddenly disappears into the cavity of the flower to fetch honey. In the Calceolarias the phenomenon is even more remarkable. The Humble-bee sits on the inflated, slipper-like lower lip, and opens the mouth by a light pressure against the upper lip. Then a nectary, hitherto hidden in the slipper-like cavity, comes to light, flap-like, and amply provided with honey. This nectary is presented to the Humble-bee just like a spoon as it sits on the lower lip. Directly the bee goes the lower lip snaps to, and the nectary disappears from view.

An interesting mechanism obtains in the flower of *Corydalis lutea* (cf. figs. 257<sup>3</sup> and 257<sup>4</sup>). The corolla here consists of four petals, one right and one left, one above and one below. The two latter are similar and applied together like two hollow hands. The right-hand petal is small and spoon-shaped, the left-hand one is the largest of all, and is produced outwards into a short spur which contains honey, whilst above it expands into a sort of brim. Access to the honey is obtained beneath this brim, and insects must enter here. To accomplish this the insect sits on the two median petals, which are applied together (fig. 257<sup>3</sup>). But to give it a better hold, each of these petals has a median flap, which may be compared to stirrups on either side of a saddle. On these the bee gets a purchase, sitting as it were on a saddle. It may be noted here incidentally that the pollen is scattered on the under surface of the abdomen of the insect by a curious lever-mechanism; also that *Corydalis* is almost unique amongst flowers in that it is lob-sided, *i.e.* the spurred petal is not in the median plane of the flower (as in the generality of zygomorphic flowers) but is inserted laterally.

Many Papilionaceous flowers have a considerable resemblance to *Corydalis*, although their flowers are constructed on quite a different plan. The Papilionaceous flower has five petals. Of these the two front ones are united together and form the "keel", the two lateral are known as the "wings", whilst the posterior unpaired one is expanded and is known as the "standard". This standard closes the entrance to the base of the flower, where the honey is concealed, from behind so that insects seeking honey must sit either on the keel or wings. In the flowers of Sainfoin (*Onobrychis*) the wings are quite small and invisible, and here the relatively big keel serves as alighting-platform. In many others, on the other hand, *e.g.* in *Coronia*, *Orobis*, *Lotus*, and *Spartium*, the wings are folded over the keel, and meeting in the middle form a sort of cushion well suited as the alighting-place of insects.

All the flowers so far described have the peculiarity that their petals are not symmetrically arranged all round. Their right and left halves agree abso-

lutely, but the upper and under halves are quite different. In this respect they are comparable to the face of a man, to the head of a vertebrate, or to the body of an insect—indeed many of these flowers resemble the heads of animals or flies, butterflies, spiders, &c. (cf. *Oncidium Papilio* and *Stanhopea Devoniensis*, Plate XIII. p. 224, and *Ophrys cornuta* and *Galeopsis grandiflora*, figs. 257<sup>2</sup> and 257<sup>5</sup>). Flowers exhibiting this kind of bi-lateral symmetry are known as *Zygomorphic*. Undoubtedly this Zygomorphy of laterally-directed flowers is connected with the formation of a landing-stage suitable for particular insects to alight upon. The Zygomorphy of *Corydalis* is peculiar, as noted at the end of the last paragraph but one.

In flowers whose opening is directed upwards, quite apart from its nature, whether it be the mouth of a narrow tube or the broad edge of an expanded plate, Zygomorphy is superfluous. Such flowers are constructed symmetrically on every side. Their petals are placed like the spokes of a wheel or the rays of a star; they have been termed *Actinomorphic*.

Such flowers, directed upwards, present a landing-stage to insects either at the periphery or at the centre. Humblebees which visit the erect, open flowers of *Gentians* (*Gentiana asclepiadea*, *pannonica*, *Pneumonanthe punctata*) alight first on the edge of the corolla, and then climb down into the wide tube, disappearing whilst they suck the honey. In the majority of cases, however, the edge of the corolla is so extremely delicate and flimsy that heavy insects, such as beetles, would not be adequately supported, but would bend the corolla right down on to the middle of the flower. Thus, in such flowers we frequently find an expanded disc-like or star-shaped stigma which forms an admirable platform, as in the flowers of *Tulipa*, *Paris*, *Opuntia*, *Papaver*, and *Argemone* (cf. fig. 243, p. 168). In *Roses*, *Buttercups*, and *Anemones* a large number of carpels



Fig. 259.—Wood Anemone (*Anemone nemorosa*).

1 Complete plant; natural size. 2 The collection of carpels from the centre of the flower; magnified.

are present in the centre forming a sort of fascicle which makes a useful platform (cf. fig. 259). Or, again, the style or stigma may be lobed or forked, the branches taking an oblique or horizontal position, thus resembling a perch (e.g. *Convolvulus arvensis* and *Siculus*). Or, it may be formed by the fascicled stamens in many upright, actinomorphic flowers, as in Myrtles, St. John's-Worts, the Australian Acacias and various Malvaceæ (at least in the first stage of flowering).

The Pinks and Scabiouses whose capitate flowers contain honey deep down are preferably visited by Lepidoptera, the flowers of Umbelliferae and Euphorbiaceæ, whose honey is exposed and easy of access, by Flies, Wasps and other short-lipped Hymenoptera. To the inflorescences of Composites and Proteaceæ, the most various insects are attracted, according to the form and position of the whole inflorescence and the depth at which honey and pollen are to be obtained. It is impossible to enumerate the various cases here for lack of space, nor, indeed, would it be desirable. One more plant, *Dryandra*, one of the Proteaceæ, deserves a brief description, however, on account of the remarkable form of its inflorescence. This plant is a low shrub, a constituent of the Australian "Scrub". Its flowers are arranged around the margin of a cup about 4 centimetres in diameter. The bottom of the cup is lined with scales only, and here collect drops of liquid secreted by the flowers, which smell like sour milk. Around the margin of the cup the long styles project like pins, bent slightly inwards. The pollen is collected at the tops of the styles at the commencement of flowering; subsequently the stigmas are developed, ready to receive pollen brought by animals from other flowers. So far as is known, this arrangement of flowers and sap is not adapted to insects. It seems probable that Kangaroos visit these flowers, stick their snouts into the excavated inflorescences to drink up the sap, and unconsciously dust their mouths round with pollen which is subsequently conveyed to the stigmas. The respective heights of the *Dryandra* bushes and of Kangaroos, and the configuration of the inflorescence compared with the snout of this animal, render the assumption a not impossible one.

The efficacy of all these arrangements for promoting the quick and easy obtaining of food from flowers by "bidden guests" is obviously much enhanced by the existence of others for the exclusion of hurtful and undesired visitants. As hurtful may be characterized all such animals whose visits interfere with or prevent the speedy transfer of pollen from flower to flower. Such are small wingless animals which must of necessity reach the honey and pollen on foot. Let us consider the case of one of these little pedestrians. Suppose it to have reached a flower and covered itself with pollen; it has now before it, in order to transfer this pollen to a stigma on another plant, a long and toilsome journey beset with dangers for the pollen, quite apart from the length of time taken. The pollen may be so easily rubbed off on the journey by hairs and other structures encountered, or it may be washed off by rain. Then, even if a second flower be attained, what are the probabilities of its being in a receptive condition? How otherwise it is with the lightly-flying insects and humming-birds! They dart from plant to plant with extraordinary rapidity and visit half-a-dozen flowers within a minute or so, thus transferring the pollen



new and fresh. Winged insects and humming-birds are ideal agents for the crossing of flowers, and are the most welcomed of all guests. But even of these fleet emissaries all are not equally welcome. Of what service is it to a plant if its pollen is not deposited on the proper spot—on the stigma where it can develop pollen-tubes—be the transfer accomplished ever so quickly? Let us suppose a tiny fly entering the flower of a Foxglove. It alights on the lower lip of the corolla and makes its way to the honey at the base of the flower where the honey is, without



Fig. 260.—*Cornus florida*; numerous small, aggregated flowers surrounded by four huge bracts, which serve at once as attractive-organs and alighting-platforms for insects. (After Baillon.)

touching the stigma or stamens placed just below the upper lip. Having satisfied itself, it retreats by the same route. What advantage does the flower get from the visit of this particular insect? None. And more than this, it has been robbed of a portion of that honey on which it relied to allure some larger animal which would unintentionally stroke the anthers and stigma with its body. By the admission of small flies to Foxglove flowers consequently no transfer of pollen would be effected. Thus we see that not all flying animals are desirable visitants; that many insects, which, in consequence of their size and shape are unable to promote a transfer of pollen, must be regarded as unbidden guests, and prevented access to the honey.

Nor are arrangements such as are indicated above wanting. Peculiar folds and

cushions, walls and gratings, brushes and thickets of hairs are present, guarding the entrance and rendering access difficult, whilst still allowing it. Large and powerful animals find these obstacles no hindrance, and readily brush them aside; small ones, however, cannot do this, but have to climb over or circumvent the obstacles. And in many cases this enforced divergence by small insects from the direct path brings about the desired result. For, in circumventing these folds and barricades and hairs, they are unconsciously led past the anthers and stigmas, contact with which is unavoidable. Thus, what would otherwise be useless visitants become welcome guests. They are conducted indirectly to the honey by these curious structures, which may, in a sense, be termed "path-finders".

A more detailed consideration of these arrangements will be given when treating of the taking up of pollen by insects, in the next chapter. Mention of them cannot be omitted here owing to the difficulty of drawing an absolute distinction between contrivances designed to lead insects by a particular route into the flower, and such as entirely exclude the unbidden guests. The same difficulty obtains between the defences erected against wingless and those against winged insects, it being in many cases not easy to distinguish between them. Consequently, the grouping of these mechanisms in the sequel cannot be entirely free from the reproach of partiality; still it will serve its purpose should it render these problems more intelligible.

First of all, we will describe the mechanisms which serve to protect flowers against little wingless marauders which creep up from the ground. Remarkable amongst these is the indirect protection afforded to the floral honey by honey secreted in the region of the foliage. This may be seen in many Balsams, especially well in the Himalayan *Impatiens tricornis*. In this plant the stipules, which stand right and left at the bases of the leaves, are modified into secretory glands. Of the two glands, one is small and rudimentary, but the other extremely well-developed. The latter is a fleshy convex disc fused partly with the base of the leaf and partly with the surface of the stem, and so disposed that insects creeping up the stem must encounter it. The honey, secreted by the tissue of this gland, collects in a drop on the hemispherical and downwardly-directed cushion of this disc. Thus are the insects tempted by the way in their ascent. They find drops of honey provided for them at the base of every foliage-leaf equalling that of the flowers in quality and surpassing it in quantity; besides which it is nearer and more accessible. The honey-loving ants lick it up eagerly, and are content not to stray further upwards. Actual observation shows that the flowers of *Impatiens tricornis* are free from ants, whilst these stipular nectaries are much frequented by them. Their presence in the flowers is very undesirable, since they could readily get at the honey there without touching the pollen or stigma. And more than this; they would not only pilfer the honey, but they would also drive away those winged insects for which the honey is prepared—the welcome guests that pollinate the flowers. We are justified on the facts in regarding this diversion of the unbidden guests as an indirect protection of the floral honey.

This secretion of honey from the stipules in *Impatiens tricornis* begins just at

the time when the plant commences flowering. This must be emphasized because the suggestion has been made that the stipular secretion serves to protect the foliage indirectly from the ravages of caterpillars, snails, and beetles. The remarkable observation has been made upon several plants, for the most part tropical, that they live symbiotically with certain small and very fierce ants. The plants afford the ants lodging in special cavities and give them nourishment in the form of sugary and albuminous secretions: the ants in return defend the foliage against the attacks of leaf-eating animals. So soon as this "standing army" of ants detects the foe it commences offensive operations, like the garrison of a fortress, and by biting and squirting formic acid frightens the invader away. In this way is protected the foliage of *Acacia spadicigera* and *sphærocephala*, *Cecropia peltata*, *Clerodendron fistulosum*, *Rosa Banksia*, and several other plants (known as *Myrmecophilous Plants*) against the attacks of leaf-eating animals. At the conclusion of this chapter opportunity will offer to describe how the flower-buds of several Composites are similarly protected against herbivorous beetles. In the case of *Impatiens tricornis*, however, the ants are no protection for the foliage; whilst the leaves are developing, no honey is secreted and no ants are present, and later, when honey is present in plenty, and the ants are licking it up, they pay no attention, even though the adjacent leaf-blades be touched or injured.

Next to the diversion of creeping animals by means of nectaries scattered over the stem and foliage may be ranked several arrangements in which the protection afforded is of a similar indirect character. Some of these have a remarkable resemblance to the devices often employed by gardeners to shield the plants in their propagating-pits and nurseries from the ravages of snails, caterpillars, centipedes, earwigs, and other noxious insects. In order to preserve a hot-house-plant from the visits of these undesirable members of the Animal Kingdom, gardeners very frequently place the pot containing the plant in question upon another low pot inverted in a shallow dish of water; thus the plant stands, as it were, on an island, and is inaccessible to the various creeping animals indicated. Similarly in a nursery the crowns of the young trees are protected against creeping vermin by tying a sticky cloth round the stem or painting the bark with bird-lime or other sticky substance. Insects attempting to climb a tree under these circumstances become imprisoned in the girdle. Caterpillars, snails, and other animals with soft integument are often excluded by attaching belts of prickly branches to the stems.

When these expedients of the gardener are compared with many of the arrangements met with in nature for the protection especially of the honey and pollen, a remarkable similarity is at once obvious. Isolation by water, prevention of access by means of sticky secretions, rings and fringes of prickles and thorns directed so as to oppose visitors on foot—such, for the most part, are the methods employed by plants to secure immunity from would-be pilferers of their honey and pollen.

*Isolation by water* obtains in the case of innumerable aquatic and bog-



plants. The flowers of Water-Lilies, of which the *Victoria regia*, represented in Plate XI., may serve as type, the flowers and inflorescences of the Flowering Rush (*Butomus*), of the Arrowhead (*Sagittaria*), of the Water Plantain (*Alisma*), of the Feather-foil (*Hottonia*), of Bladderwort (*Utricularia*), Villarsia (*Limnanthemum*), Frog-bit (*Hydrocharis*), Water Soldier (*Stratiotes*), and of many other plants are amply protected by the belt of water which their situation involves. Flies and beetles which come through the air for honey and pollen are welcome visitors, promoting, as they do, a crossing of the pollen; snails, centipedes, &c. are, on the other hand, kept back by the water. The basins of water formed by the bases of the leaves in the Teasel (*Dipsacus*) and *Silphium perfoliatum* (figured, vol. i. p. 239), serve a like purpose, as also do the collections of water in the funnel-like sheaths of the leaves of many Bromeliaceæ (*Æchmea*, *Billbergia*, *Lamprococcus*, *Tillandsia*, &c.), though this is supplemented by other advantages derived by these plants from the receptacles of water in question (cf. vol. i. p. 241).

More frequently even than by water the flowers obtain immunity from these visitors by *sticky secretions*. The substance formed in many cases resembles bird-lime in properties, though its chemical constitution is not fully ascertained; in others it is allied to gum-arabic, or cherry-gum; whilst in others again it is a resin or a mixture of resin and mucilage known by the name of gum-resin. Occasionally this purpose is served by latex, which readily escapes from the brittle tissues and coagulates on the surface into an adhesive substance. This last method obtains particularly in certain Asclepiads, and in many species of Lettuce (e.g. *Lactuca angustana*, *sativa*, *Scariola*). The involucre scales which inclose the flower-heads of these plants are smooth and tense, and abound in latex. No obstacle prevents creeping insects, especially ants, from climbing up to this point; but as soon as the ants reach these scales on their way to the flowers, and touch the turgid investing cell-layers, they rupture the walls of the latex-tubes (which in some cases actually project as tiny hairs on the surface) with the claws of their feet, and the milk runs out in little droplets. Their feet and abdomens are smeared with latex, and when the ant bites at the substance of the scales in self-defence its head also becomes involved in the sticky mess. It seeks to free itself of this encumbrance in a variety of ways, but the result of all these struggles is merely a further rupturing of the epidermis and discharge of latex, which adds to the embarrassment of the ant. Some of these creatures manage to escape and drop to the ground, others, not so fortunate, are glued in the coagulating latex, where their dead bodies may be seen decorating the involucre of the capitulum.

The other adhesive substances mentioned arise either from certain circumscribed cells of the flat epidermis of the stem, or else definite projecting structures known as glands, glandular hairs, capitate hairs, &c., are specialized for this purpose. In the case of flat epidermal cells, the secretion is passed out from the cells and collects between the inner and outer layers of the external wall, in other words,

under the cuticle. The cuticle is gradually raised up like a blister till it bursts and the sticky matter escapes. Such portions of the stem or flower-stalk resemble limed twigs, and might have been painted with the viscid substance. In the case of definite glands, the secretion, for the most part, diffuses through the walls to the surface, though in some cases the blister-method may obtain here also. Sometimes the secretion is freed by actual rupture of the delicate walls of the glandular cells.

Sticky secretions as protection for flowers against creeping animals occur most frequently on the flower-stalks, or on the main axis of the inflorescence. The popular names of several plants indicate at once their sticky character, as, for instance, the Catchfly (*Silene*), and the Viscid Lychnis (*Lychnis Viscaria*). So also, with their botanical names indicative of their adhesive character and of the insects caught by them, e.g. *Silene muscipula*, *Roridula muscipula*, and the specifications *viscidus*, *viscosus*, *viscosissimus*, *glutinosus*, and the like—names frequently occurring amongst the Scrophulariaceæ, Labiatae, Caryophyllaceæ, and in the genera *Ledum*, *Cistus*, *Linum*, *Aquilegia*, and *Robinia*. That the protection afforded by these limed stems is essentially floral is particularly well shown in the Caryophyllaceous genera *Dianthus*, *Lychnis*, and *Silene*. The lower portion of the stem in these plants (e.g. *Dianthus viscidus*, *Lychnis Viscaria*, *Silene muscipula*) is green, and shows no trace of the sticky brown coating which is first met with below the pair of leaves subtending the flowering axes. And here it is only the upper portion of the internode, the portion in the immediate neighbourhood of the flowers that is sticky (cf. fig. 238, p. 154).

More frequent than a simple sticky coat is the presence of glands and glandular hairs on the flower-stalk, or on the outside of the flower itself, to which little animals climbing up the plant become adherent. Of this condition numerous examples are represented in fig. 261.

A rarely-occurring condition obtains in the flowers of *Cuphea micropetala* (fig. 262). The petals in this plant are reduced to tiny scales inserted at the top of niche-like excavations of the calyx (fig. 262<sup>4</sup>). The calyx is tubular and coloured, 22–28 mm. in length, and 6–7 mm. in diameter; at the base behind the ovary it is expanded into a honey-receptacle. The ovary is relatively large and obliquely placed, forming a sort of “elbow” at the point of articulation of the style which touches the upper wall of the calyx-tube (262<sup>2</sup>). Since the side-walls of the calyx are in close contact with the ovary, the honey-receptacle is cut off from the general cavity of the flower, as it were, by a plug. Right and left in the ovary, however, are two grooves, slightly wider in front; these form (with the calyx) two tiny canals, about half a millimetre in diameter, by which access may be had to the honey-cavity behind the ovary; usually these canals are more or less filled with honey (cf. figs. 262<sup>2</sup> and 262<sup>3</sup>, the latter showing the orifices of the two canals and elucidating the relations of the parts). To obtain the honey, flying insects must introduce their probosces into

one of these canals. The admission of little ants to these flowers, insects useless for purposes of pollination, and likely to block up the honey-orifices for authorized visitors, would be disadvantageous. The arrangements which prevail for the exclusion of ants are so elaborate that one would think that the honey of *Cuphea micropetala* was for them quite irresistible. The mouth of the flower is rendered quite inaccessible to ants and other minute creeping insects by a fringe of tufts, each bearing a number of divergent sticky bristles (262<sup>1, 2, 4</sup>). These bristles form in the aggregate a *chevaux-de-frise*, guarding the mouth of the

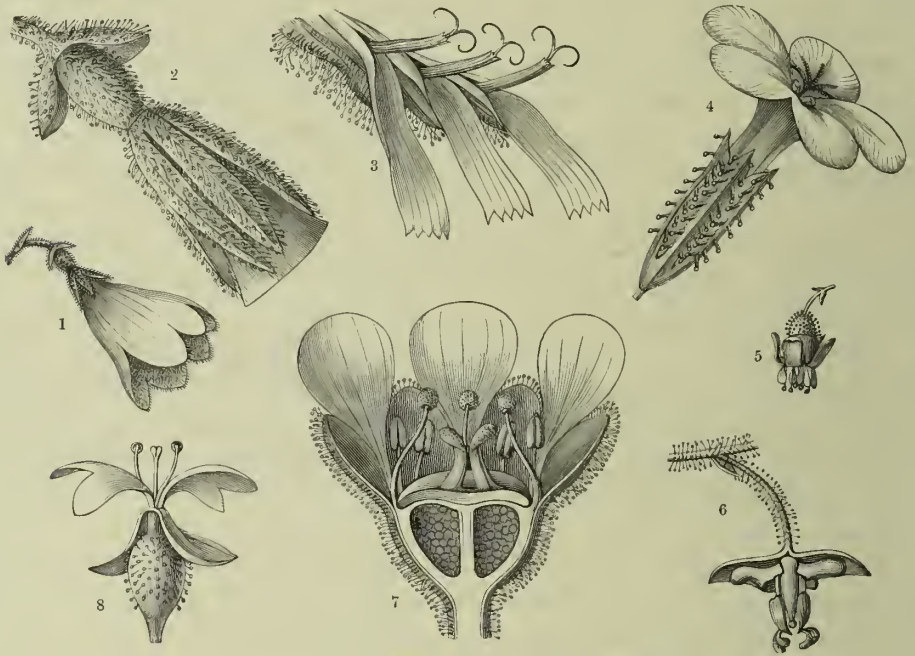


Fig. 261.—Sticky glands as a protection to Flowers.

- <sup>1</sup> Flower of *Linnaea borealis*. <sup>2</sup> Calyx, inferior ovary and bracteoles of *Linnaea* (considerably enlarged). <sup>3</sup> Three ligulate florets from the capitulum of *Crepis paludosa* showing the glandular scales of the involucre immediately below them. <sup>4</sup> Flower of *Plumbago europaea*; the ribs of the calyx are provided with stalked sticky glands. <sup>5</sup> Flower of *Ribes Grossularia*; stalked glands shown on the inferior ovary. <sup>6</sup> Flower of *Epimedium alpinum*; the pedicel is glandular. <sup>7</sup> Section of flower of *Saxifraga controversa* with sticky glands on pedicel, ovary, and calyx. <sup>8</sup> Flower of *Circea alpina* with inferior ovary covered with glands. <sup>9</sup> natural size; all the other figures magnified.

calyx-tube, through which these small visitors cannot penetrate. Flying insects, however, which can reach the honey hovering at the mouth of the flower, and such as can use the projecting stamens or stigma as support are not impeded by the bristles, and are, so to speak, welcomed by the flowers of *Cuphea micropetala*.

In addition to these plants, provided with adhesive glands about the flower and its accessory structures, others exist in which the whole of the foliage is sticky. As examples may be mentioned various Primulas (*Primula glutinosa*, *viscosa*, *villosa*), Saxifrages (*Saxifraga controversa* and *tridactylites*), Crassulaceæ (*Sedum villosum*, *Sempervivum montanum*), and several Steppe-plants (*Cleome*



*ornithopodioides*, *Bouchea coluteoides*, &c.). That their stickiness saves the flowers of these plants from many undesirable visitors there can be no doubt. Often enough the dead bodies of small creatures that have ventured upon them may be seen adhering to the foliage. In some of them the plant actually supplements its normal nutrition by a diet of these insects' bodies, and the glandular hairs would appear to subserve the same functions as the similar structures in *Drosophyllum lusitanicum*, and the various species of Sundew and Butterwort already described (cf. vol. i. pp. 153–156).

This is the place to mention the waxy coatings of flowering axes and pedicels, which, in a number of plants, guard the flowers from the approach of small creeping

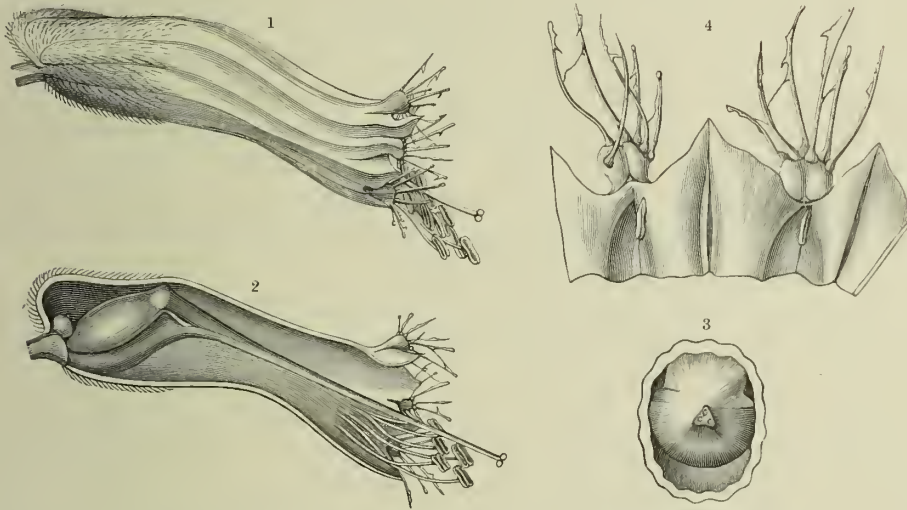


Fig. 262.—Sticky Bristles at the edge of the Calyx as a protection to Flowers.

<sup>1</sup> Flower of *Cuphea micropetala*. <sup>2</sup> Longitudinal section of the same flower. <sup>3</sup> Transverse section of the same flower at the height of the insertion of the style upon the ovary. <sup>4</sup> Small portion of the calyx-limb showing the sticky bristles in little tufts. 1, 2, 3  $\times 2$ ; 4  $\times 8$ .

insects—though, of course, in many cases they serve another function. The bloom on the catkin-bearing twigs of the Violet Willow (*Salix daphnoides*) and Caspian Willow (*Salix pruinosa*) undoubtedly plays this part. For these Willows, which are dioecious and largely dependent upon bees for the transfer of their pollen, it is of importance that the honey should be reserved for useful visitors and not needlessly wasted. Ants and the like, climbing up to the catkins and attempting to traverse the wax-covered twigs, slip and lose their footing, and tumble down to the ground again.

It is not improbable, though no observations are to hand, that the stems and branches of *Melianthus*, *Dentaria*, *Sanguinaria*, *Fritillaria*, &c., by their slippery coating of wax provide a similar protection to the flowers which are rich in honey in each case.

It is especially hard chitinous insects, such as ants, whose progress is arrested by sticky or waxy surfaces in the neighbourhood of the flower. Against snails and

slugs such arrangements are less efficacious. Indeed, these creatures are but little incommoded by adhesive secretions, for they can overcome any obstacles of the kind by themselves secreting a copious slime. Towards spines, prickles and stiff bristles, snails, and indeed all soft-bodied animals are extremely sensitive. Thus whilst ants and the like can travel unimpeded over the rough leaves and prickly heads of Teasels, the soft-bodied organisms avoid hispid and spinose surfaces. Stiff bristles, teeth, and prickles, then, situated in the neighbourhood of the flowers, form a good protection against visitors of this class. It should be mentioned that these animals—snails and caterpillars—do not take especially honey or pollen, but devour indifferently the petals, stamens, and carpels. It is hardly necessary to describe these spiny mechanisms in detail here, as the subject has been already treated for the case of foliage (vol. i. p. 433), and the two phenomena have very much in common. Two features, however, may be pointed out as having a direct bearing on the matter in hand; firstly, where flowers as well as foliage are protected by spiny structures against creeping animals, the number of these structures increases markedly in the neighbourhood of the flowers; secondly, it often happens that spines placed immediately about the flower serve not only to exclude the unbidden guest, but at the same time as “path-finders” to direct the welcome honey-sucking insect, so that it shall dislodge the pollen and disturb the stigma.

This latter feature applies in marked degree to the sheathing bract-like investments of many flowers which must be surmounted by insects before they can reach the honey. The small capitate flowers of Composites, Scabiouises, and many Pinks are very rich in honey; but this honey is only for insects which visit the flower from above, where the stamens and stigmas are displayed. The illegitimate removal of honey—from below or from the side—must be prevented. Now many insects, especially bees and humble-bees, when they come across honey inclosed in a delicate sheath bite through the wall and steal the honey, as it were, through a back-door. Liability to this class of pilfering must be excluded by tough, impenetrable sheathing structures around the basal, honey-containing regions of the flower. Such structures are well shown on the Teasel-heads and capitula of many Pinks, in which the nectariferous portions of the flowers are protected by imbricating scales. The strongest humble-bee cannot pierce them, and the only alternative is to obtain the honey in the legitimate manner.

It is very generally assumed, and in several cases on adequate grounds, that the inflated calyces and sheaths of bracts which inclose the flowers of many plants serve to protect the honey from marauding of the kind indicated. Thus, in a case in which the honey is distant 20 millimetres from the wall of an inflated calyx, it cannot be reached by the humble-bee whose proboscis is only 8 millimetres long by means of a hole bitten in the calyx. Humble-bees will visit the flower by the ordinary way and get the honey thus with less expenditure of energy. But such relations do not generally obtain; in a majority of cases the interval between the inflated calyx, and the honey is less than 8 millimetres, so that the average humble-bee could get the honey by biting

through. As a matter of fact, however, it is usually easier for the bee to get the honey in the ordinary way, and these arrangements of inflated calyces are rather of the nature of protections against creeping insects, ants, and the like than humble-bees. There are in the European Flora some 300 plants whose flowers are robbed by humble-bees biting through the calyx or corolla. For several of them, which depend entirely upon insects for the transfer of their pollen, this burglarious proceeding is fatal. Fertilization is not accomplished; their ovules atrophy and propagation by seed is impossible. Such plants have flowered in vain. Herein lies a contradiction to the otherwise marvellous harmony which exists between the configuration of plants and animals, a contradiction only explicable on the assumption that these plants, whose honey is taken without concurrent pollination, date back to a time at which humble-bees were absent from the district in question. A Catchfly (*Silene Pumilio*), the flowers of which are industriously visited by humble-bees, occurs in the Eastern Alps (Taurus). The great majority of these bees decline to enter the flowers properly, but, hanging on to the inflated calyx, bite a hole in it and take the honey. The Catchfly rarely sets seeds, and one may see hundreds of plants together, not one of which has ripened a fruit, although they flowered freely during the summer. At the present time this Catchfly has a very restricted distribution in the Alps, and even in districts where it occurs is sporadic. Nor does it propagate with any vitality. The same is the case with another Catchfly (*Silene Elizabethæ*, of the Southern Alps) and with several species of Aconite and Corydalis. Any one familiar with the facts, although he may not be an enthusiastic supporter of current hypotheses as to the history of the vegetable world, must admit:—(1) That these endemic species are becoming extinct in the Alps. (2) That the humble-bees are to blame for this in that they steal the honey without doing the plants any service in return. (3) That these plants date back to a time at which humble-bees did not frequent the regions where they grow, and at which the flowers needed protection only from creeping insects.

The bulk of the arrangements, so far described for the exclusion of unbidden guests, occur outside the cavity of the flower, and are directed against creeping animals which climb up from the ground. Those, on the other hand, directed against undesirable winged-insects are situated chiefly *inside* the flower and take the form of hairs and fringes. These may be arranged either into irregular tufts and woolly plugs, or with greater regularity, into lattice-works, cages, and crowns of hairs. Thus we find a woolly thicket occupying the whole cavity of many bell-shaped and urceolate corollas, as in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*, fig. 263<sup>1</sup>), or the hairs are confined to the tubular portion of the corolla as in the little alpine *Primula minima*. In the Alpine Roses (*Rhododendron hirsutum* and *ferrugineum*) and in several of the Honeysuckles (*Lonicera nigra*, *Xylosteum*, and *alpigena*, fig. 263<sup>7</sup>), the stamen-filaments and parts of the corolla contribute hairs, which, in the aggregate, make a thicket defending the honey. Often the corolla is quite smooth inside, and the bases of the stamens alone are provided with flocks of hair which screen the nectaries, as in *Atropa*, *Lycium*, and *Polemonium*. In the well-



known climber *Cobæa scandens*, the insertion of each stamen is inclosed in a regular felt, and these five felty tufts form, as it were, a sort of diaphragm which cuts off the honey-secreting, basal region of the flower from the main cavity of the bell (see fig. 263<sup>5</sup>). Again, in the Tulip (fig. 263<sup>4</sup>), each stamen secretes honey at its



Fig. 263.—Tufts of Hair as a Protection to Flowers.

- <sup>1</sup> Longitudinal section of the flower of the Bearberry (*Arctostaphylos Uva-ursi*). <sup>2</sup> Longitudinal section of flower of Red Valerian (*Centranthus ruber*). <sup>3</sup> Transverse section of the same flower. <sup>4</sup> Portion of the flower of *Tulipa sylvestris*. <sup>5</sup> Longitudinal section of flower of *Cobæa scandens*. <sup>6</sup> Longitudinal section of flower of *Daphne Blagayana*. <sup>7</sup> Longitudinal section of flower of *Vinca alpigena*. <sup>8</sup> Longitudinal section of flower of *Vinca herbacea*. <sup>9</sup> Single stamen of *Vinca*. <sup>10</sup> Style and stigma of *Vinca*. <sup>6</sup> Natural size. All the other figs. magnified.

base in a little depression of the filament on the side directed towards the perianth. Tufted hairs completely cover the nectary, so that insects have to lift the whole stamen to get honey. In *Daphne Blagayana* (fig. 263<sup>6</sup>) the stalked ovary is enveloped in hairs, by which the honey formed at the base of the flower is protected from unbidden guests.

In the flowers of *Vinca herbacea*, indigenous to the Steppes of the Black Sea (cf. figs. 263<sup>8, 9, 10</sup>), the apices of both stamens and stigma are provided with tufts of hairs which interlock and close the mouth of the corolla-tube, as it were, with a plug of cotton-wool. One of the most curious of these arrangements is found in the Red Valerian (*Centranthus ruber*, fig. 263<sup>2</sup>). The corolla-tube is some 12 millimetres long and scarcely 1 millimetre in diameter; it is divided longitudinally by a membranous diaphragm into two tubes, of which the upper contains the long style, whilst the lower one, produced into a spur, contains the honey. This lower tube is lined throughout its entire length with hairs, which, although they present no obstacle to the introduction of a proboscis, prevent little insects from creeping in and stealing the honey. As may be seen in fig. 263<sup>3</sup>, these hairs project a considerable distance into the interior of the tube.

Hedges or palisades of erect elastic hairs or fringes, inserted on circular cushions in tubular corollas, are not infrequently met with. These fringes stand straight out into the tube and conceal its cavity. They are sometimes quite at the mouth of the tube, as in *Veronica officinalis*, sometimes a little distance down the throat, as in the Vervain (*Verbena officinalis*), or quite at the base, as in *Acanthus*, *Phlox*, *Horminum*, and *Prunella*. Fringed scales in rings are found in the flowers of many Genetians and Passion-flowers. In several Rutaceæ, *Haplophyllum*, for instance, hairs from the bases of the stamens form a sort of lattice-work at the base of the flower, whilst, in a species of *Monotropa*, the cushion beneath the stigma bears radiating hairs which, reaching as far as the corolla, make an elegant grating. The honey in *Swertia perennis* is secreted in little cup-like depressions near the bases of the petals. The margins of the cups are fringed with hairs which converge, and are so interwoven that the cups are protected by little cages. These few examples are typical of a vast series of lattices, gratings, and the like, occurring in flowers to shield the honey.

Protection from undesirable visitors is also obtained in a great variety of ways by the bending, twisting, or convergence of various parts of the flower, so that the honey is hidden in grooves and special cavities. Amongst these are included flowers with long, narrow tubes, into which the delicate proboscis of a butterfly can be introduced, but which are too narrow for small insects to crawl into; also, such as have various projections, cushions, and lobes of the corolla which narrow or subdivide the aperture; finally, closed flowers which can only be opened by powerful insects, and such as have their stamens so crowded that little insects cannot obtain access to the honey. Several of these have been already described and figured (p. 180, 181).

We may also regard the periodic display of attractions to insects as being, in a way, of the nature of a protection against unbidden guests. The subject has been already alluded to (p. 156) in detail, so we need only add that the arrangements obtaining in many moth-visited Caryophyllaceæ are also found in *Zaluzianskia lychnidea*, a Scrophularineous plant from the Cape. Its flowers have a long honey-secreting tube and spreading limb (as in *Silene*), the ten lobes of which are dark



purple underneath and brilliant white above. By day the lobes are furled, so that their dark inconspicuous sides are shown, nor is there any scent or other attraction; consequently it remains unnoticed by day-flying insects. But in the evening the lobes of the corolla fold back, and the white flowers are now conspicuous, whilst a strong Ylang perfume is given off to attract moths. In *Hesperis tristis*, *Pelargonium atrum* and *triste*, there is a similar periodic exhalation of perfume, though the inconspicuous petals always remain in one position. But here the scent is the main attraction, and at nightfall numerous moths are attracted by the delicious



Fig. 264.—Capitula of *Serratula lycopifolia* protected by Ants (*Formica exsecta*) from the attacks of a Beetle (*Oxythyrea funesta*)

perfume of Hyacinths which is then apparent. *Hesperis* is visited by great numbers of Owlet-moths (Noctuæ) of the genus *Plusia*, which transfer the pollen from flower to flower.

*Silene nutans*, already so fully described (p. 154), may be regarded as the type of the plants now under consideration. It is additionally interesting in that it possesses a double protection against unbidden guests. By its unattractive character during the daytime it is protected from diurnal flying insects, whilst the sticky secretion on its flowering axis keeps off crawling animals such as ants.

So much has been said in this chapter concerning ants as undesirable visitors, and of the means for their exclusion, that this is an appropriate place for a brief account of certain instances in which they are of real service in guarding and



protecting flowers. We have already seen how ants are diverted from visiting flowers by honey secreted on the foliage, and how, in certain instances, an actual symbiosis obtains between the plant and the ants. Especially do these ants protect the foliage from the attacks of leaf-eating animals. This reciprocal service, performed by the ants, is in no wise of the nature of gratuitous philanthropy, it is done in their own interests. The lodging and the food which the ants obtain from the plant constitute two of their most important necessities, consequently it is worth their while to protect the "goose that lays the golden eggs".

A similar state of affairs is met with on the capitula of several Composites indigenous to South-eastern Europe, e.g. *Centaurea alpina* and *Ruthenica*, *Jurinea mollis*, and *Serratula lycopifolia*—the last of which is figured opposite. The young capitula of these Composites are particularly liable to the attacks of devouring beetles, especially of *Oxythyrea funesta*, which bites big holes in the heads, destroying crowded flower-buds and involucreal scales without the least difficulty. To meet this danger a garrison of warlike ants is employed. Honey is secreted from big stomata on the imbricating scales of the still-closed capitula in such quantities that one can see a drop of it on every scale in the early morning, whilst later in the day, as the water evaporates, little masses, or even crystals of sugar are to be found. This sugar, either in its liquid or solid form, is very palatable to the ants, which habitually resort to these capitula during the period of its secretion. And to preserve it for themselves they resent any invasion from outside. If one of the aforementioned beetles appears they assume a menacing attitude. They hold on to the involucreal scales with their last pair of legs and present their fore-legs, abdomen, and powerful jaws to the enemy, as shown in fig. 264. Thus they remain till the beetle withdraws, if necessary hastening its retreat by squirting formic acid in its direction. Then they quietly begin to feed on the honey again. Ants of the same species do not fight amongst themselves on these Composites, although as many as ten to fifteen specimens of the ant *Camponotus Ethiops* live on each capitulum of *Jurinea mollis*, and about the same number of *Formica exsecta* on the heads of *Serratula lycopifolia*.

As soon as the florets on the heads begin to open, the secretion of honey diminishes and ultimately ceases. No longer do beetles come to devour them, nor is there any further need for protection. The garrison is withdrawn, the ants going away in search of other, younger flower-heads.

#### TAKING UP OF POLLEN BY INSECTS.

Having obtained in the last chapter a general survey of the contrivances in connection with the advent and reception of insects at the portals of flowers, we are now in a position to describe the means whereby insects, after reaching the flowers, are covered with the pollen there awaiting them.

The simplest case is that where the insects rove and climb about the flowers, and so get powdered all over with pollen. This happens in innumerable Umbelli-

feræ, Dipsacæ, and Caryophyllacæ, which, owing to the association of large numbers of flowers in umbels, fascicles, spikes, or capitula, afford a playground richly furnished with slender waving stamens where pollen is easily to be shaken or brushed off the anthers on every hand, although each single blossom only contains a few stamens. In the case, too, of the single flowers of Roses, Anemones, Peonies, Poppies, Magnolias and Opuntias, which are well supplied with stamens, insects pushing between the anthers or feasting on pollen that has dropped upon the petals get covered on head, thorax, abdomen, wings, and legs with the floury pollen. This is true also of the spathes of Aroideæ and of fig-inflorescences which are haunted by midges, beetles, and gall-wasps, and deposit their pollen on these visitors as they crawl out of their temporary refuge in the manner described on pages 156-160. Mention was made in the same chapter of the fact that insects, after being imprisoned for a time in the flowers of the *Aristolochia*, are quite covered with pollen when they emerge. The phenomenon, which was there merely glanced at, is so remarkable that it is worth while to give a somewhat fuller account of it. In the widely-distributed species of Birthwort represented in fig. 257<sup>s</sup> on p. 226, and named *Aristolochia Clematitis*, the way into the enlarged base of the flower is over a convenient ligulate alighting-place and through a dark and comparatively narrow passage lined with hairs. The free extremities of these hairs point inwards, *i.e.* towards the inflated chamber, and they permit visitors from the insect-world—small black midges of the genera *Ceratopogon* and *Chironomus*—to pass into the chamber. But once inside, the midges are obliged to reconcile themselves to remaining imprisoned for a couple of days. The hairs, whilst offering no hindrance to ingress present a bristling stockade of points to insects seeking to escape (see fig. 257<sup>o</sup>). At first the midges endure their captivity with complacency, for the warmth of their dungeon suits them, whilst the succulent cells lining its walls afford a certain amount of nutriment. On the second or third day of imprisonment the lateral walls of the anthers, which are adnate to the stigmatic column, open and let the mealy pollen fall to the bottom of the chamber. The pollen is also acceptable to the midges for food, and they feast upon it liberally. At last, however, they become restless and look for a means of exit, and in bustling actively about the chamber, they cover their entire bodies with pollen. After this the hour of their deliverance is no longer deferred. The hairs in the narrow passage wither and collapse, leaving a free exit, and the midges all be-powdered with pollen hasten to leave the flowers. That they retain no unpleasant recollection of their temporary confinement may be inferred from the fact that they have no sooner escaped from one flower than they creep into another, which has only just reached the stage at which entrance becomes possible. This latter circumstance must be emphasized in order to arrive at a complete understanding of the significance of the curious phenomenon just described. The moment the flower is accessible to insects, the stigma is ready to receive the pollen whilst the anthers are still closed. When the midges proceed from an older to a younger flower, they brush against the latter's stigma, which is situated right in front of the inner end of the dark passage, and deposit

the pollen they have brought with them upon it, and may thus bring about cross-pollination between the different flowers.

In many cases insects visiting the interiors of flowers only get smeared with pollen on the upper or the under parts of their bodies, or at particular spots merely, and the adherence of the pollen ensues on their rubbing against the anthers which are situated along the insect's route when it enters or leaves the flower. This process takes place in a great variety of ways. In one case, the only part dusted with pollen is the proboscis; in another, the head; in a third, the shoulders or back; in a fourth, the upper surface of the abdomen; in a fifth, the under surface of the abdomen. There are instances also in which the pollen is only brushed off by the peculiar collecting-brushes on the legs of bees which were spoken of in the last chapter. Again, reference was made on page 153 to the remarkable case of the small moth *Pronuba yuccasella*, which has the first joint of its maxillary palp metamorphosed into an organ of seizure, and by means of that implement collects the pollen from *Yucca*-flowers, makes it up into a ball and holds it fast in front of its body (see fig. 240<sup>5</sup>, p. 157).

If stamens, projecting out of the flower or situated on the floral threshold, serve as a place for insects to alight on, as, for instance, in the flowers of *Funkia*, *Viper's Bugloss*, *Figwort* and *Monkshood* (*Funkia*, *Echium*, *Scrophularia*, *Aconitum*), pollen adheres to the underneath part of the insect's body the moment it settles, or as it crawls towards the interior of the flower. In one of the species of *Alpine Rose* (*Rhododendron Chamæcistus*) and in the *Germander Speedwell* (*Veronica Chamædrys*; see fig. 257<sup>1</sup>, p. 226), insects visiting the flowers, which are directed laterally, grasp the exserted stamens with their front legs as if they were perches. The stamens are arranged so as to bend downwards and inwards when touched, thus they become almost instantaneously applied to the under surface of the insect's body, which becomes smeared with the pollen. Great quantities of pollen adhere to the under parts of insects in the case of *Composite* inflorescences. Shortly after the opening of the corollas, the style bearing an external load of pollen is exserted from each of the little tubular and ligulate florets composing the capitulum in this group, and, owing to the fact that large numbers of these florets invariably open simultaneously, numbers of styles laden with pollen project close together from the discoid head. A largish insect settling on a capitulum may therefore be dusted with the pollen of numerous florets at once. As he twists and turns about on the disc of the inflorescence inserting his proboscis into one floret after another a lot more pollen is brushed off on to the under surface of his body, and he finally leaves the capitulum with an abundant freight.

The transference of pollen to insects takes place in the *Lady's Slipper Orchid* (*Cypripedium*) in a manner altogether peculiar. Here it is only one of the shoulders of the visitor that receives the pollen. We will briefly describe how this happens in the case of the *European species* (*Cypripedium Calceolus*). The floral envelope of this Orchid (see fig. 267<sup>1</sup>) consists of six leaves, one of which is shaped like a slipper, and has its deep cavity furnished at the bottom with hairs full of



sap. Sometimes little drops of nectar are also secreted by the cells composing these hairs. Certain small bees of the genus *Andrena* are in the habit of entering the cavity to feast on the hairs. Three ways are open to them, viz. the two small orifices in the background on either side of, and close to, the column, and the large oval opening in the middle of the slipper and in front of the column. They choose the last and slip under the broad, rough stigma to the bottom of the slipper where they feed on the succulent cells of the hairs. After a time they wish to escape into the open air again, but that is not so easy. The edges of the large central opening are inflected (see fig. 267<sup>2</sup>), and so fashioned as to be unscalable, and the bees have no choice but to make use of one of the two little exits at the back of the slipper.

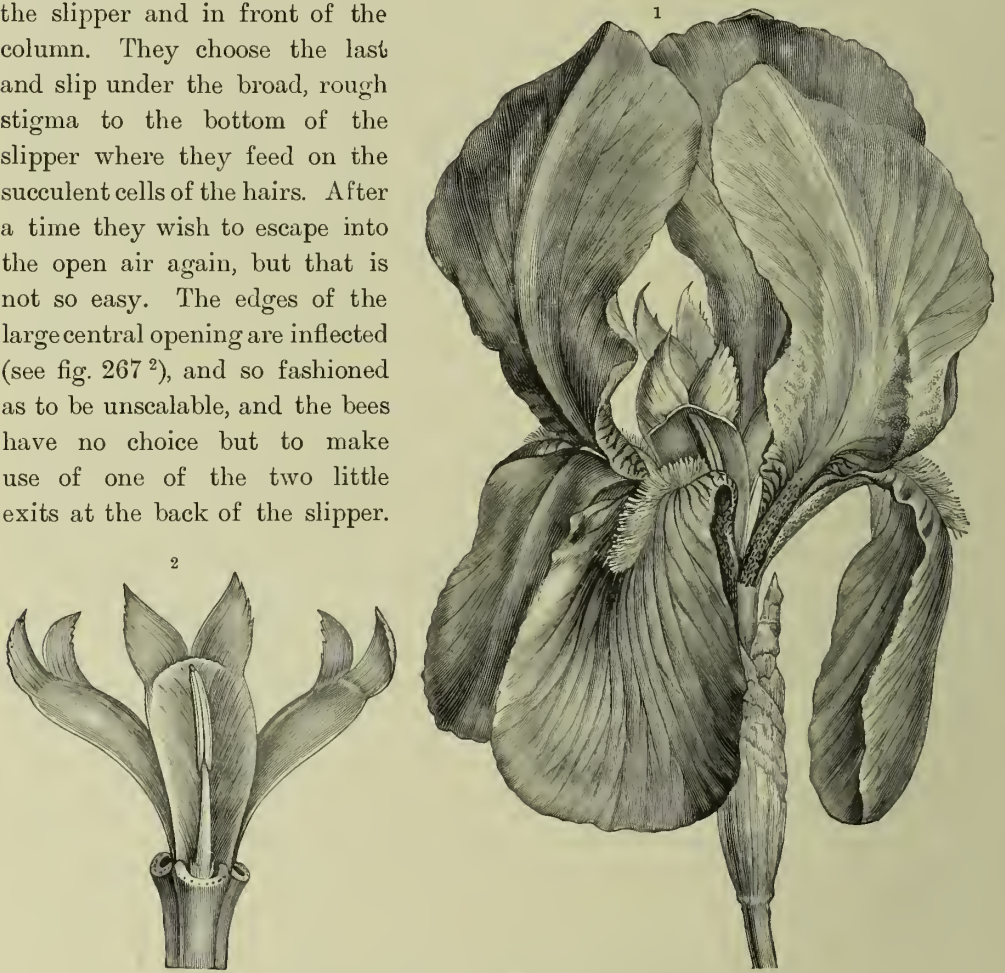


Fig. 265.--Contrivances for loading insects with pollen.

<sup>1</sup> Flower of an Iris (*Iris Germanica*), with three segments of the perianth reflexed and three erect. On each of the former is a strip of yellow hairs which stand out conspicuously from the violet background of the perianth-segment, and serves as a guide to insects entering the honey-containing tube of the perianth. <sup>2</sup> Upper half of the perianth-tube showing the three passages leading to the honey. Above each passage is a stamen with a long, linear anther facing outwards, and arching over each stamen is one of the three bi-lobed petaloid stigmas. The perianth-lobes have been removed.

Even through these escape is not altogether easy, the bees being obliged to squeeze through the narrow opening. The result is that one shoulder brushes against the soft, viscid pollen of the anther which forms the inner border of the orifice. The last act in the story is the entrance of the insect with its shoulder covered with pollen into another *Cypripedium* flower, whose rough stigma is thereupon immediately besmeared with pollen.

Instances are very common in which insects in seeking honey brush the upper parts of their bodies against the anthers, thus covering their backs with pollen. Humble-bees, when they visit Iris flowers (fig. 265), settle on the hairy ridges of the outer deflexed perianth-segments as the most convenient alighting-places, and thence proceed to the honey-containing canals of the perianth-tube. They thus pass under one of the petaloid stigmas, and at the same time under the corresponding stamen, which is so placed and curved as to exactly fit the dorsal surface of the humble-bee. The pollen is thus brushed off on to the insect's back. Similarly, bees entering the gaping flowers of *Gladiolus*, of the Dead Nettle (*Lamium*) and other Labiates rub their backs against the anthers, which are concealed close underneath the upper lips, and carry away pollen on that part of their bodies only. The same holds good in the case of the humble-bees which slip into the large bells of Gloxinia, clamber up to the honey in Foxglove flowers (*Digitalis*), or venture into the jaws of

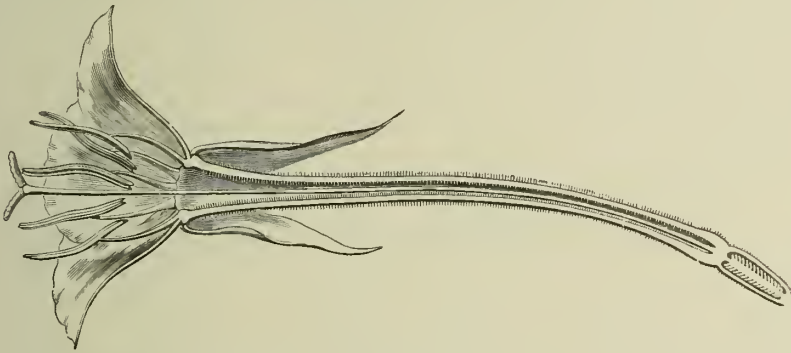


Fig. 266.—Longitudinal section through a flower of the Evening Primrose (*Enothera biennis*).

the Snapdragon or Toad-flax (*Antirrhinum*, *Linaria*). In the flowers of *Linaria* two pairs of large anthers are situated close under the arch of the upper lip, and the pollen discharged by them is in the form of two round balls, which are both detached at once from the fissures in the anthers upon the occasion of an insect's visit, and are carried away to other flowers on the back of the intruder.

The laterally-directed flowers of the Evening Primrose (*Enothera*; see fig. 266) are visited by moths which insert their probosces into the long floral tubes as they flutter about in front of the flowers. In so doing, the moths brush their heads against the anthers surrounding the entrance to the flower-tubes, and cover them with pollen. The head is also the part affected in the case of the Sun-birds (*Cynnyridæ*) which take the rich brown honey from the lower, bowl-shaped sepal of *Melianthus* flowers (see fig. 258<sup>12</sup>, p. 227), and in the process bring their heads into contact with the anthers above it.

The adaptation of flowers with a view to ensuring that insects seeking their honey shall brush off the pollen with some part of their bodies, whether back, belly, shoulders, head, or at least the proboscis, is of so manifold a character that it is impossible, having regard to the scope of the present work, to deal with all the contrivances coming under this category. Only a few of the most striking

examples will be described, and as they are to a certain extent identical with those already referred to in connection with the subject of the protection of honey, we need not enter into them at so great length as would otherwise be necessary. In the first place, there are the flowers which are furnished inside with prickles or sharp, stiff bristles. It is well known that honey-sucking insects, such as humblebees, are very careful of their probosces, keeping them in special grooves in their bodies whenever they are not in use, and taking pains when they do use them not to thrust them against rigid points on account of their liability to injury. Thus a flower, furnished with sharp prickles or bristles, only admits an insect's proboscis by a well-defined path. The intruder avoids the points, and is thereby prevented from entering by a route which would not involve its rubbing against the anthers—and is induced to take a course inevitably accompanied by the deposition of pollen on its back, head, or proboscis. This occurs, for instance, in some Cruciferae (*Braya alpina*, *Malcolmia Africana*; see fig. 267<sup>6</sup>), where the insects are guided to the honey between two series of rigid upright bristles borne by the ovary, and are obliged to brush their heads and probosces against the pollen-laden anthers. The same thing happens in *Leonurus heterophyllus* (see fig. 267<sup>7</sup>), a Labiate, which has a patch of sharp prickles in the throat just behind the under-lip. Insects desirous of possessing the honey secreted at the base of the flower, and at the same time of avoiding the prickles, are obliged to insert their probosces close under the upper-lip, and are thus brought into contact with the pollen-covered anthers there situated. In several small alpine Gentians, such as *Gentiana glacialis* and *G. nana*, the entrance to the interior of the flower is covered by four valves with lacerated margins which are so pliable as to form no barrier to the entrance of the stronger kinds of insect. But no anthers would be brushed by their probosces if they were to enter by that way, and the possibility of such an occurrence must, therefore, be obviated. The fringed edges of the valves closing the throat are for this purpose thickly studded with minute prickles. Insects reject the route as too risky and prefer to enter between the points of insertion of the valves whence passages of adequate size and quite free from danger lead to the honey. In passing along them the insects brush the anthers which are situated close by. The compulsory condition imposed on insect-visitors that they should rub the pollen off with their probosces, and occasionally with the tops of their heads and front parts of their thoraces, depends in many cases on the fact that there is only one approach leading to the honey, and the external orifice of this passage is straitened by a ring-like callosity, or by the presence of flaps or scales, whilst the anthers are situated round the orifice, or just underneath it. This arrangement is found, for example, in many Boragineae, Oleaceae, Primulaceae, and Polemoniaceae. The hawk-moth, which sucks honey in the autumn from the flowers of the Phlox, a plant belonging to the Polemoniaceae, and butterflies, which feast in the spring on the sweet juices of Lilac-flowers load only their probosces with pollen, for, in consequence of the form and disposition of the various parts of the flowers, this part alone comes into contact with the anthers.



The same mechanism exists in so-called "revolver-flowers," *i.e.* flowers which exhibit within their outer portals the open ends of a number of small tubes resembling the barrels of a revolver. These tubes are arranged in a great variety of ways. In Bindweeds and Gentians (*Convolvulus*, *Gentiana*) the filaments are adnate to the corolla-tube and project in the form of ridges towards the central ovary, and so divide the main tube into four or five separate pipes. In some Geraniums and several species of Flax (e.g. *Geranium Robertianum*, *Linum viscosum*), a ridge arises from the middle of each petal and projects towards the centre of the corolla,



Fig. 267.—Contrivances for ensuring the deposition of pollen on insect-visitors.

- <sup>1</sup> Flower of the European species of Lady's Slipper (*Cypripedium Calceolus*). A bee (*Andrena*) is forcing its way out through one of the holes at the side of the stigma and smearing its shoulder with pollen. <sup>2</sup> Longitudinal section through the labellum and column of the Lady's Slipper. <sup>3</sup> An *Andrena* on the wing. <sup>4</sup> Flower of Grass of Parnassus (*Parnassia palustris*) with the front sepals, petals, nectaries, and stamens cut away; of the stamens which are visible three are despoiled of their anthers, the fourth has assumed a position placing the anther in the middle of the flower. <sup>5</sup> Single nectariferous scale from the flower of *Parnassia*. <sup>6</sup> Flower of *Malcolmia maritima* with the front sepal, the two front petals, and two stamens cut away; the visible portion of the ovary bearing a longitudinal row of stiff bristles (white). <sup>7</sup> Longitudinal section through the flower of *Leonurus heterophyllus*. <sup>8</sup> Flower of *Kerneria saxatilis* in the first stage of development, seen from above. <sup>9</sup> The same at a later stage of development, seen from above. <sup>10</sup> The same flower, seen from the side, with the front sepal and the two front petals removed. <sup>11</sup> Vertical section through a flower of *Trollius Europaeus* (Globe-flower). <sup>1</sup> and <sup>2</sup> nat. size; the rest  $\times 2-8$ .

dividing it into five tubes, which surround the styles and stamens in a circle. In Flaxes of the group *Cathartolinum* each petal is swollen in the middle and attenuated, and concave near the edges; the juncture of the concave margins of adjacent petals gives rise to a flat canal which leads to the floral receptacle. The corolla-tube of the Winter Cherry (*Physalis*) is fluted by five grooves, which, together with the villous filaments facing them, form as many tubes. In all these

“revolver-flowers” the anthers are so placed with their pollen-covered faces in front of the mouths of the tubes, that insects inserting their probosces are bound to rub against them.

The flowers of the Wild Mustard (*Sinapis arvensis*), *Diplotaxis*, and several other Cruciferous plants have anthers, which, after dehiscence, execute spiral twistings with the object of turning the face covered with pollen away from the stigma, and placing it near the spot where insects insert their probosces for the honey. In other Cruciferae, with flowers somewhat resembling “revolver-flowers” in structure, although the approach to the honey is not straight through a tube, the stamens exhibit characteristic bendings of the filaments with a view to bringing the anthers into the line of entrance to the nectar. Thus, for instance, in the flowers of *Kernera saxatilis* (see figs. 267<sup>8, 9, 10</sup>), honey is only to be found on the two narrow sides of the compressed ovary, although there are petals all round the ovary. Supposing all the filiform filaments, whether in front of the narrow or of the broad sides of the ovary grew straight up, only the anthers borne on the former would deposit their pollen on the honey-sucking insects. In order to render the anthers situated opposite either of the broad sides of the ovary which are destitute of honey liable to be stroked by intruding insects, their filaments are bent at right angles, as is shown in figs. 267<sup>9</sup> and 267<sup>10</sup>. By this means all the dehiscent anthers of the flower are brought into such a position as to be necessarily rubbed by insects when they come to suck the honey. Movements of stamens, directed to the same end, are also observed in numerous Caryophyllaceae, Ranunculaceae, Saxifrageae, Crasulaceae, and Droseraceae. The floral structure in the Caryophyllaceous plants coming under this category is similar to that of “revolver-flowers”; the petals are unguiculate, that is to say, they are composed of an inferior very narrow part inserted in the tubular calyx, called the claw or *unguis*, and a flat expanded region above the calyx called the *lamina*. A groove runs down the middle of the claw to the floral receptacle, and at the upper end of the groove, where butterflies are to introduce their probosces, the lamina is sprinkled with bright-coloured patches or speckles, and is furnished sometimes with scales arranged in pairs, or something else of the kind to make the entrance conspicuous, and regulate and facilitate the introduction of the proboscis. In these Caryophyllaceae the anthers, just after dehiscence, are so placed in relation to the entrance that butterflies must necessarily smear their heads and probosces with pollen as they thrust the latter organ along the grooves. After that has happened, the filaments bend to one side or stoop down beneath the laminae of the petals, and then other stamens come into play, their anthers being held, as the first were, in front of the grooves running down the petals. In the Ranunculaceae—*Eranthis*, *Helleborus*, *Isopyrum*, *Nigella*, *Trollius* (see fig. 267<sup>11</sup>)—a large number of stamens surround the central multiple pistil in several whorls. They are themselves encompassed by a circle of very small trumpet-shaped or tubular petals filled with honey, the so-called nectaries, and these are in their turn surrounded by large floral leaves, white, yellow, red, or blue in colour, which descriptive Botanists have designated as petaloid sepals. Shortly

after the interior of the flower becomes accessible, owing to the opening of these sepals, the anthers belonging to the outermost whorl of stamens dehisce. Their filiform filaments have in the meantime undergone elongation, inflection, and torsion to the extent necessary to bring the anthers exactly over the opening admitting to the little cups full of honey. Insects cannot suck the honey without brushing against these anthers. The next day the stamens of the first whorl move in an outward direction towards the sepals, their place being at once taken by the stamens of the next whorl nearer the centre of the flower. By the third day these, too, are reflexed and replaced by the members of the third whorl; and the process continues until all the stamens in turn have set their anthers over the nectaries. The punctuality and exactitude with which the whole series of operations is carried out is most extraordinary.

The same phenomenon may be observed in the flowers of the Grass of Parnassus (*Parnassia palustris*). Only here the number of stamens is limited to five, and one anther at a time is set in the way of alighting insects as is shown in fig. 267<sup>4</sup>. The honey is secreted in two small oblong depressions on the inner face of certain curious fimbriate leaf-structures which are inserted between petals and stamens (267<sup>5</sup>). If an insect in search of honey alights from above on the middle of the flower, it is certain to brush its proboscis against the particular anther which has set free its pollen that very day, and is itself in close proximity to the approach to the honey. The Grass of Parnassus possesses in addition another extremely interesting contrivance correlated with the movements of those insects, which, instead of alighting from above, settle on the edges of the petals. When such an insect moves from the margin of the expanded petals towards the nectaries it encounters a barrier in the form of railings composed of the radiating arms of the nectariferous scales. This barrier is not, however, insurmountable; its radiating arms do not secrete any viscid substance or terminate in sharp points, but are surmounted by round yellow knobs, resembling pins' heads (see fig. 267<sup>5</sup>). The insect easily climbs over this obstacle without hurting itself, and then finds itself on the side of the scale where the nectaries are. But in doing so, it is brought so nearly to the middle of the flower that it is sure to touch the anther, which, having opened that very day, occupies the position commanding the passage to the nectar. We have here an instance of the adaptation of a flower to different visitors. Both those which settle from above and those which crawl from the edges of the petals are obliged to brush against the effective anther in the middle of the flower and besmear themselves with its pollen.

In all these cases the pollen pours in copious quantities from the anthers and forms either puffy masses which cling to the gaping loculi, or else a viscid mantle clothing the slender style, when that organ has been used to sweep it out of a tube of syngenesious anthers. Insects, on visiting the flowers, come into immediate contact with the pollen, it being in no way covered or wrapped up, and being obtruded so directly in the path that to avoid it would be impossible. In the next series of plants there is a certain amount of difference in this respect. The pollen



is not accessible direct, but is concealed in tubes or recesses, and the covering must be removed before an insect can be besmeared. In the composite flowers of the genera *Onopordon* and *Centaurea*, to which belongs, amongst others, the well-known Corn-flower (*Centaurea Cyanus*), the anthers are borne on slender filaments, and, as in all Compositæ, are connate into a tube, in which is concealed the upper portion of the style. The dehiscence being introrse, the pollen is deposited on the style. In the majority of Compositæ, the style then grows in length and pushes the pollen up beyond the top of the tube. But this is not the case in *Onopordon* or *Centaurea*. No elongation of the style occurs, and the pollen remains concealed in the tube. If, however, an insect sets foot on the central part of the capitulum and comes into contact with the stamens as it clammers over the florets of the disc, the filaments immediately contract, drawing back the sheathing anther-tube and leaving the pollen exposed on the top of the style, which is then brushed against by the under surface of the insect. The same result is achieved by different means in certain Papilionaceæ. The well-known *Cytisus*, *Melilotus*, *Trifolium*, *Onobrychis* are instances of one group. The front pair of petals, which is known as the keel, and serves as an alighting-place for insects, forms a receptacle with a very narrow opening at the top. In this are concealed the ten stout, partially connate filaments, and the anthers borne by them. When a humble-bee settles on the keel and inserts its proboscis into that part of the flower where honey is to be found, the keel is pressed down by the insect's weight, and the anthers are in consequence exposed, whilst the pollen resting upon them is rubbed off on to the under surface of the insect. The moment the insect leaves the flower the keel springs back to its former position, and once more conceals the anthers which, as a rule, have only parted with a portion of their pollen. The same process is repeated on occasion of each fresh visit, and as many as four different insects may thus be dusted with pollen from the same flower. In *Lathyrus*, *Orobus*, *Pisum*, *Vicia*, the phenomenon is in the main the same, but these plants have a special brush developed in connection with the style which sweeps the pollen out of the keel, where it has been deposited by the anthers, at the same moment as the insect alights on the flower. The insect is thus certain to carry away pollen on the under parts of its body.

The transference of the pollen in the Hemp Nettle (*Galeopsis*) and Monkey-flower (*Mimulus*) to the bodies of insects is also attended by a curious phenomenon. A stamen of *Galeopsis* is shown in fig. 216<sup>19</sup>, p. 91. The corolla is bilabiate, and beneath the arch of the upper lip are two pairs of stamens, one pair behind and the other in front of the stigma, which is bilobed, and has the property of shutting together its two component flaps in response to contact. Each of the anthers of the pair behind the stigma is box-like, and divided by an internal septum into two compartments capped by lids. If a needle is inserted into the flower so as to touch the anthers, the lids spring open, disclosing the pollen, which sticks to the needle; a similar action occurs when an insect visits the flower.

These cases, where the pollen has first to be uncovered by the insect before it can be carried away, are not more remarkable than those wherein pollen-masses

are concealed in niches, and are caused to adhere to the bodies of intruding insects by means of a special organ, and are then drawn out of their hiding-places. This method of transferring the pollen is especially characteristic of Orchids, and is extremely interesting. It will be worth while to consider it in some detail in connection with a few well-known instances, and for that purpose it will be necessary to begin with a general description of the peculiar structure of the flower in Orchids. In all species of Orchidaceæ the ovary is inferior, and at the flowering season resembles a pedicel. It bears at the top two tripartite whorls of floral leaves, one standing just above the other. Two segments in each whorl are alike in form, whilst the third is different. The difference is most conspicuous in the case of the odd segment of the inner whorl, and it is called the lip or *labellum*. Often it really resembles a lip, but not uncommonly it assumes the shape of a sabot, boat, or basin, whilst, in other cases, it is like an outstretched tongue, or even the body of a spider or insect (see fig. 257<sup>2</sup>, p. 226 and Plate XIII.). The labellum is frequently lobed, and may also be fringed or slit up into long curling strips. In fact it exhibits an endless variety of configuration, and to it is mainly due the extraordinary appearance characteristic of Orchids. The ovary itself is produced in most Orchids above the two perianth-whorls, and rises up in the middle of the flower as the so-called *column*. This structure, which bears the stamen and the stigmatic surface, is always opposite the labellum, so that the approach to the bottom of the flower lies between the two. There are *two* stamens in the few Orchids allied to the already-mentioned Lady's Slipper (*Cypripedium*; see figs. 267<sup>1</sup> and 267<sup>2</sup>), but throughout the others only *one* stamen in each flower develops pollen. The filament can only be identified by careful examination and dissection of the flower; externally it is not visible. Usually the anther or pair of anthers is imbedded in pits or recesses in the column, or is adnate to one face or to the top of the column. In the flowers of the Helleborine (*Epipactis latifolia*, fig. 268<sup>2</sup>), and many other Orchidaceæ, on either side of the one stamen, which has a fully-developed bilocular anther, may be seen an abortive stamen in the form of a triangular tooth. The column bears, in addition to the stamens, a stigmatic surface corresponding to the tips of the three carpels. In the group of Orchids represented by the Lady's Slipper (*Cypripedium*) all three are capable of taking up pollen; in all other Orchids only two stigmas are receptive, and they are usually merged together into a single disc or plate; the third stigma being transformed into the so-called *rostellum*, a structure which plays an important part in connection with the processes now to be described. The rostellum assumes the most various forms in different Orchids, and special relations subsist between it and the anther. In many cases the rostellum is a beak-like structure, situated betwixt the solitary stamen and the stigmatic surface; it marks, so to speak, the frontier between these two structures. Certain portions of the rostellum disintegrate, forming a tough and extremely sticky mass like bird-lime, which, in most cases, takes the form of a wart. The anther is bilocular. The loculi contain each a clavate pollen-mass or *pollinium*, and open betimes—often indeed, before flower is open. After dehiscence

the pollinia may be seen peeping out of the longitudinal slits in the loculi with their narrower extremities connected with the adhesive portion of the rostellum (as in fig. 268<sup>2</sup>). The manner in which this connection is established varies greatly, according to the species, and cannot be discussed here; all we need note is the fact that the union is so strong that the two pollinia are drawn out of their hiding-places and carried away by any object which, coming into contact with the rostellum, removes the viscid mass from it. The Broad-leaved Helleborine (*Epipactis latifolia*), a plant of wide distribution in Europe, exhibits extremely well all the peculiarities of Orchids above referred to (see figs. 268<sup>2</sup> and 268<sup>3</sup>). The upper part of the labellum is excavated, and contains a copious supply of honey. Above the labellum is the quadrangular stigma (fig. 268<sup>2</sup>) borne by the column, and surmounting this is the wart-like and projecting rostellum (a white dot in the figure), whilst the anther crowns the column. The two pollen-masses developed in the anther are connected with the viscid portion of the rostellum. Fig. 268<sup>4</sup> shows what the pollinia look like when they are drawn out of the anther. The honey secreted in the cavity of the labellum is easily accessible to insects with short probosces, and the flowers of Helleborine are therefore much frequented by wasps. I have selected *Vespa Austriaca* for illustration, as I have often observed wasps of that species on the flowers. On alighting the insect holds on with its legs to the embossed parts of the lip and proceeds to lick up the honey filling the cavity, beginning at the bottom and working up to the top. During the latter part of the operation its forehead must inevitably come into contact with the viscid projecting rostellum, which at once adheres to it (see fig. 268<sup>5</sup>). In withdrawing from the flower, when the feast is over, the wasp draws the two pollen-masses attached to the viscid rostellum out of the anther-loculi, and flies away into the open air adorned with this curious head-dress (fig. 268<sup>6</sup>). Not satisfied with the meal afforded by a single flower, it straightway seeks another and behaves here in the same manner as it did on the first occasion. During the time of flight from one flower to another the pollinia, sticking to the wasp's forehead, undergo a gradual tilting forward, the sticky gland remaining fixed at the same spot, but the pollinia becoming depressed; as a consequence of this change in their position, the pollinia are not shoved into the anther of the next flower the wasp visits, but are pressed against the quadrangular stigma (see fig. 268<sup>7</sup>). This depression of the pollinia is much better marked in many other common Orchids, however.

In all essential respects the process above described is common to the majority of Orchids where the labellum has a downward inclination and there is only a single anther; but great variety prevails in respect of accessory details, as indeed is to be expected, when we consider the wide divergencies existing in the forms of the flowers and of their insect-visitors. A brief reference to two of the most striking modifications is all we can give here. The greatest variation is exhibited, as we said before, by the labellum and the rostellum. In some genera—in the Twayblade (*Listera*), for example—the part of the lip which contains the honey is not bowl-shaped, but in the form of a long, narrow furrow, and the secretion



is licked up by small beetles. In other instances the back of the lip is produced into a spur lined with cells full of sweet juice, to which insects obtain access by piercing the walls of the cells. The genus *Orchis* affords an example of this. Honey of a sort peculiarly attractive to butterflies is secreted in the tubular spur in other cases, such as *Gymnadenia* and *Habenaria* (see fig. 258<sup>9</sup>, p. 227).

Two separate particles of viscid matter are often produced on the rostellum, each being in connection with one only of the pollen-masses (e.g. *Habenaria*



Fig. 263.—Withdrawal and deposition of pollinia in the flowers of an Orchid

Flowering spike of the Broad-leaved Helleborine (*Epipactis latifolia*) upon which a wasp (*Vespa Austriaca*) is alighting.

<sup>2</sup> A flower of the same seen from the front. <sup>3</sup> Side view of the same flower with the half of the perianth towards the observer cut away. <sup>4</sup> The two pollinia joined by the sticky rostellum. <sup>5</sup> The same flower being visited by a wasp, which is licking honey and at the same time detaching with its forehead the tip of the rostellum together with the pair of pollinia. <sup>6</sup> The wasp leaving the flower with the pollinia cemented to its head; the pollinia are erect. <sup>7</sup> The wasp visiting another flower and pressing its forehead with the pollinia (which in the meantime have bent down) against the stigma. <sup>1</sup> nat. size; the other figures  $\times 2$ .

*chlorantha*, the Large Butterfly Orchis). Insects then frequently only draw one of the pollen-masses out of the anther, instead of both, as they leave the flower. In species of the Twayblade genus (*Listera*) the rostellum is scale-like and arches over the stigmatic surface. At the commencement of the flowering period it is not connected with the pollinia, but the moment it is touched it exudes a drop of viscid fluid which sticks, on the one hand, to the body touching

it, and, on the other, to the pollinia surmounting the rostellum, and, hardening almost instantaneously, cements them together. The flowers are visited by small Hymenoptera belonging to the genera *Cryptus*, *Ichneumon*, and *Tryphon*, and still more frequently by little beetles of the genus *Grammoptera*. When an insect of any one of these genera lands on the labellum and proceeds to lick the honey-secreting furrow from the bottom to the top, it finds itself, towards the conclusion of its meal, in contact with the projecting edge of the rostellum. In a moment the pollen-masses are cemented to the forehead of the insect in the manner described, and are subsequently carried away upon a visit to another flower.

Strange to relate, the viscid masses sometimes adhere to the eyes of insects, although there can be no doubt that their power of vision is thereby curtailed. This occurs, in particular, in those Orchids where the anther-loculi and pollinia diverge from one another towards their bases and are connected with two separate viscid masses pertaining to the rostellum. In the flowers of *Habenaria montana* the pollinia are inclined to one another at an angle of  $70^{\circ}$  and form a kind of yoke under which it is necessary for butterflies to insert their heads if they want to suck the honey from the long spur. Thus the viscid discs, and, through their intervention, the pollinia are certain to attach themselves to either side of the intruder's head, and the eyes are frequently the spots where the adhesion happens to be effected. The genus *Habenaria* is also of interest inasmuch as it illustrates the fact that the particular minor variations in floral structure which are used to differentiate species always possess some special significance in relation to the visits of insects. The *Habenaria Hookeri* of the New World differs from the *Habenaria montana* of the Old World in having in the middle of the stigma a projecting lobe, the presence of which results in the formation of two entrances to the spur containing the honey. A butterfly visiting the flower only inserts its proboscis into one of the two passages, and therefore comes into contact with only one of the viscid discs and carries away but a single pollinium. Yet another arrangement is found in *Habenaria bifolia*, the Lesser Butterfly Orchis, which is widely distributed in Europe and Asia. In this species the pollinia lie nearly parallel and above the entrance, and they usually adhere simultaneously to one eye of the Sphingidæ which visit them (see fig. 258<sup>11</sup>, p. 227), or to the base of the proboscis in the case of nocturnal Lepidoptera (Noctuæ of the genera *Agrotis*, *Hadena*, and *Plusia*). In the various species of *Gymnadenia* the pollinia adhere to the sides of the probosces of the small Noctuæ which suck their honey, whilst in the Musk Orchis (*Hermidium Monorchis*) they become attached to the front feet of such little Hymenoptera and beetles as come to lick their sweet store. A long series of contrivances showing a wonderful correlation between the forms of flowers and those of flower-seeking insects might be added to these examples.

At the time when insects visit the flowers, the Orchids hitherto referred to, all of which have erect inflorescences, have their labella turned towards the

ground owing to the stalk-like inferior ovaries being twisted (*cf.* Plate XIII.). Only quite a few Orchids, on the other hand, retain the parts of the flower in the same positions, after the bud is open and ready for insects, as were occupied by them in the bud. *Epipogium aphyllum*, a remarkable plant, which has been already referred to in respect of its peculiar mode of life (see vol. i. p. 111), may be taken as a type of this group. As shown in fig. 257<sup>10</sup>, p. 226 of the present volume, five of the perianth-segments of *Epipogium aphyllum* are long and narrow and slightly incurved. These segments inclose a space in the same sense as the curved fingers of a hollow hand may be said to do so, and in the middle of the space the column presents itself in the shape of a slightly ascending platform for insects to alight on. Arching over it is the sixth leaf of the perianth, the labellum, which resembles a cowl or helmet and causes the whole flower to look somewhat like that of Monkshood. Honey is concealed in the interior of the cowl, and in order to reach it the humble-bees which frequent this Orchid are obliged to crawl up the landing-stage with their bodies in contact with it, that is to say, with the column bearing the stigma and anther. The separate parts of the flower here are in the reversed position as compared with ordinary Orchids, where the labellum is the lowest member. The column bears the anther at its lower extremity, then comes the rostellum, which develops an extremely sticky disc, and still higher up, the steeply-sloping wall of the stigma (see fig. 257<sup>12</sup>). The oval pollinia are attached to the viscid disc of the rostellum by long ductile filaments or pedicels (see fig. 257<sup>13</sup>), and are covered over by a membranous hood, the anther-case. When an individual of the species of humble-bee named *Bombus lucorum*, a frequenter of shady woods, alights on the column of a flower of *Epipogium aphyllum* and proceeds to crawl from the lower edge of that structure towards the honey concealed in the galeate labellum, it does not at once come into direct contact with the pollinia, they being covered by the hood-like anther-case, but the viscid disc of the rostellum immediately adheres to the under part of the insect's body. Afterwards, when the bee leaves the flower, the anther-cap is thrown back and the two pollen-masses attached to the viscid disc are drawn out of their niches and carried away (fig. 257<sup>13</sup>). The manner of their transference to other flowers will be discussed in the next chapter.

In many respects similar to these Orchid-mechanisms for promoting a transfer of the pollen are those prevailing in the flowers of Asclepiadaceæ, where the pollen masses are fastened by special organs of attachment to the feet of insects. Here again the pollen is in the form of pollinia connected together in pairs, and one cannot look at them without being reminded of the analogous structure in Orchids (see fig. 269<sup>4</sup>). On nearer inspection, however, important differences are discovered to exist. In the first place, the little knob ("corpusculum") connecting the two pollinia is not soft and viscid as in Orchids, but is a hard, dry implement with two arms capable of holding any small delicate object by gripping it like a clip; secondly, the pollinia are not clavate or of pasty consistency, but are in the form of



shining horny leaflets; and thirdly, the two pollinia which are attached to the clip-like body by ligulate strands belong to two adjacent stamens instead of to a single one. A transverse section through the flower of *Asclepias Cornuti* (see fig. 269<sup>3</sup>) shows in the centre a five-sided column; adnate to each of its sides is a tumid bilocular anther with membranous wings running down its lateral margins. The wings are not appressed to the column, but are reflexed, and stand out in pairs, with the free margins of the two wings in each pair converging towards one another. This produces the same effect as if the anthers coating the central column were slit through longitudinally in front of every corner of the pentagon. Owing to the fact that the swollen part of each anther bears a curious excavated structure, it comes about that the pollen-producing portions of the anthers are nowhere visible externally save the membranous wings or the five apparent slits, as is shown in

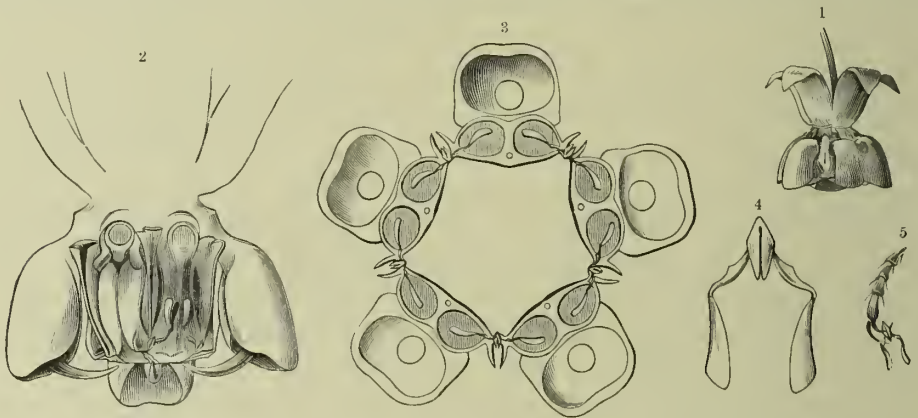


Fig. 269.—Clip-mechanism for fastening the pollinia of *Asclepias Cornuti* to the feet of insects.

- <sup>1</sup> Flower of *Asclepias Cornuti* seen from the side. <sup>2</sup> The same magnified and with two staminal appendages and the front wall of an anther cut away. <sup>3</sup> Transverse section through the same flower. <sup>4</sup> Corpusculum (the clip) with two pollinia. <sup>5</sup> Foot of an insect with pollinia fastened to it by the clip. <sup>1</sup> nat. size; the other figures  $\times 2.5$ .

figs. 269<sup>1</sup> and 269<sup>2</sup>). The hollow staminal appendages are full of honey, and each is embellished by a central process shaped like a horn. At the back of every one of the five slits is a little clip-like organ from which proceed ligulate strands connecting it with the pollinia in the adjacent loculi of two different anthers (loculi have vertical shading in fig. 269<sup>3</sup>), the pollen-mass in the left loculus of the anther to the right of the slit being thus associated with the pollen-mass in the right loculus of the anther to the left of the slit. The abundant honey in the staminal appendages emits a scent perceptible from afar, and attracts numberless insects to the flowers. The honey, being stored in a very superficial position, is accessible to insects with short probosces, and, therefore, the chief visitors besides hive- and humble-bees are wasps and Fossores, and these bright-coloured glossy insects—especially the splendid *Scolias* (*Scolia hæmorrhoidalis*, *S. quadripunctata*, *S. bicincta*)—are a beautiful sight as they hover about the blossoms. During the time when the honey is most abundant the flowers are either nodding or pendent, and they offer no convenient place for the insects to alight upon, or from which

they can comfortably suck the honey. All parts of the flower are smooth and slippery, and the only way in which an insect can support its weight is by inserting its claws in the slits between the anthers. In endeavouring to take firm hold, the insect draws its claw from one end of the slit to the other, and so becomes attached to the clip-like organ at the back. When the insect's foot is withdrawn the two pollinia adherent to the clip are dragged out of their niches. One of the claws on that foot is then seen to be wedged between the arms of the clip, whilst the two pollinia are suspended from it (see fig. 269<sup>5</sup>).

The subsequent history of the pollinia does not strictly belong to the subject of this chapter, but it will be convenient to follow them to their destination. The pollen-masses must be conveyed to stigmas of other flowers. The question is, where are these stigmas to be found? The pentagonal central column, surrounded by the five anthers, contains the ovary in its interior. The approaches to this organ lie through the so-called stigmatic chambers, which are situated close beneath the truncate end of the column, and open outwards. The chambers are concealed in the slits, just as were the clip-like organs, and insects occasionally come across them as they move their claws about in the recesses. If the foot inserted by an insect has pollinia already attached to it, they are thus introduced into the slit in a new flower, and as the insect feels about for firm support it thrusts the pollinia into the stigmatic chamber. When the foot is subsequently withdrawn, the ligatures attaching the pollinia to the little clip are broken, and the pollinia are left in the chamber, whilst the actual clip maintains its grip of the claw. A second organ of the kind with its pollinia may become attached to the insect's foot on this occasion, and the process may indeed be repeated a number of times. Insects caught after visiting flowers of *Asclepias Cornuti* have often been found to have from five to eight of these clips fastened to a single foot.

Other members of the Asclepiadaceæ have essentially the same mechanism, though differences in detail of course occur. Very interesting is the result of cultivating the asclepiad *Araujia albens* (*Physianthus albens* of gardeners) in regions in which it is not indigenous. This plant is a climber from S. Brazil and Buenos Ayres, and being an ornamental plant is cultivated in gardens in various parts of the world. In its own country it is visited normally by humble-bees, and the curious phenomenon to be described has not been reported as occurring there. But in other localities its sweet-smelling, tubular flowers are visited by hosts of moths, which are apparently unacquainted with the mechanism of the pollen-masses, &c., and get trapped by their probosces in the slit-like notches, which are present between the anther-wings. These wings are rigid, and the slit narrows upwards, and moths visiting the flowers for honey get their probosces jammed in the slits. The result of their struggles to free themselves is only to fix their probosces the tighter in the narrow end of the slit, and the moths die a lingering death with their heads concealed in the tubes of the corollas, and their abdomens projecting. Reliable testimony of this moth-catching propensity of *Araujia albens* is forthcoming from Massachusetts (Providence), from Italy (Cagliari), and from

the Orange Free State. The victims include *Plusia precatationis*, *P. Gamma*, and *P. chrysitis*, *Picris Brassicæ*, *Deilaphila Euphorbiæ*, &c.

This clamping of pollinia to the feet of insects is quite unique amongst phenomena of the kind observed in the whole realm of plants, and it would be scarcely surprising if people who have not seen the operation with their own eyes were to look upon it as the offspring of a botanist's imagination. There are, however, in the same category, four other cases of behaviour equally calculated to excite astonishment in the observer, and these are all the more remarkable from the fact that in them the transference of pollen to the bodies of insects is effected by means of special movements of different parts of the flower. The insects do not dust off the pollen by coming into immediate contact with it, but their entrance into a flower causes certain changes in the position of the various parts resulting in the pollen being sprinkled, thrown, or rubbed upon particular parts of the intruder's body.

I do not like comparing these contrivances in plants to the devices of human ingenuity; but the analogy existing between the various kinds of mechanism which effect the transfer of pollen and machines, invented by man, is so close that it would be affectation to refuse to take advantage of the fact that the action of these contrivances in plants can be rendered much more easily intelligible by describing them in terms which plainly indicate their resemblance to simple appliances in use in every household. We shall, therefore, differentiate the various kinds of mechanism for loading insects with pollen, which still remain to be discussed, into those provided with piston-apparatus; hammers, or percussive apparatus; springs, or explosive apparatus; and sprinklers.

To begin with, let us take the *piston-apparatus* in Papilionaceæ. In very many though not all Papilionaceæ the two lateral petals, called *alæ* or wings, converge towards their upper margins, along which they are in contact, so that they form a convex saddle arching over the keel. This arrangement may be seen, for instance, in *Coronilla*, the Horse-shoe Vetch (*Hippocrepis*), the Lupine (*Lupinus*), the Rest-harrow (*Ononis*), *Anthyllis*, and in the Bird's-foot Trefoil (*Lotus corniculatus*; see figs. 270<sup>1</sup> and 270<sup>2</sup>), the last being the species here selected for illustration. The wings are connected with the keel in a peculiar manner. Near the base of each wing is a projecting fold which exactly fits into a socket in the corresponding half of the keel (see figs. 270<sup>3</sup> and 270<sup>4</sup>). Thus wings and keel are locked together, and every pressure upon the pair of *alæ* is transmitted to the keel. Consequently when a hive- or humble-bee sets itself astride on the saddle-ridge formed by the wings, not only is the latter pressed down, but also the keel; and this movement is accompanied, to the astonishment of the observer, by the extrusion of a pasty vermicular mass of pollen through a small opening at the conical apex of the keel, and by the simultaneous adhesion of the pollen to the insect's belly, or sometimes to its legs. The process of expulsion is shown in figs. 270<sup>5, 6, 7</sup>, where a number of stamens lying close together are seen to be thickened into clubs at the part just below the anthers. This bundle of stamens



shuts off at the free end of the keel a hollow cone which is open at the apex only, and the action of the stamens within the cavity is just the same as that of the piston inside a pump. When the keel is depressed by a force acting in the direction of the arrow (fig. 270<sup>6</sup>), the stamens, being fixed, are forced further into the conical cavity and push part of the pollen stored in it through the small orifice at the top. When the pressure ceases the keel returns to its former position. It has been ascertained by careful observations that the process of pumping pollen from a particular flower may be repeated eight times, provided that the keel is not pressed down too low, and that when the keel is depressed beyond a certain

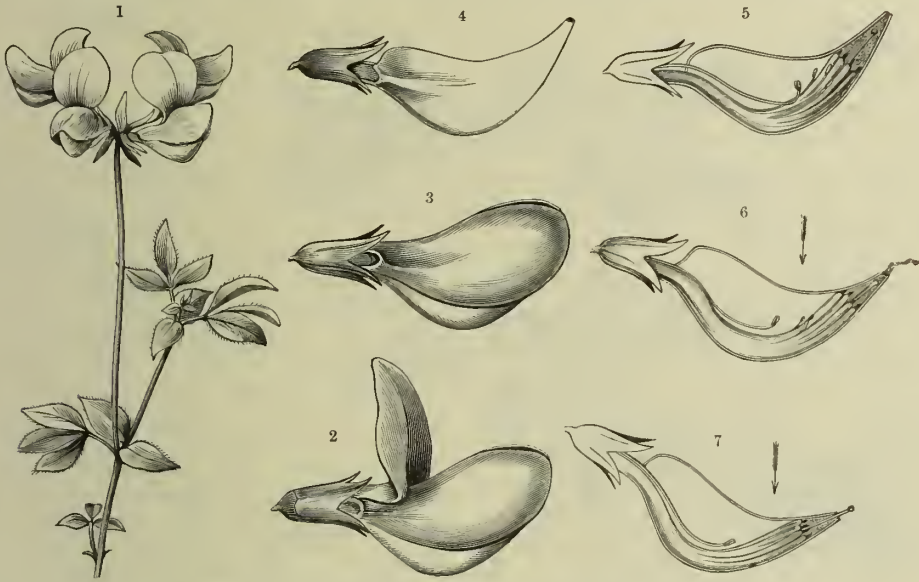


Fig. 270.—Apparatus for pumping pollen on to the bodies of insects.

<sup>1</sup> *Lotus corniculatus*. <sup>2</sup> Single flower of the same  $\times 2$ . <sup>3</sup> The same flower with the standard removed. <sup>4</sup> The same flower with the standard and the wings removed so as to expose the keel. <sup>5</sup> One component leaf of the keel removed; in the interior of the keel are seen the stamens, the longer ones clavately thickened towards their free extremities; the conical cavity above the anthers (which are empty) is full of pollen, and the style and stigma are embedded in the mass of pollen. <sup>6</sup> Depression of the keel in the direction indicated by the arrow, in consequence of which pollen is pumped out of the orifice of the conical cavity by the bundle of clavate filaments. <sup>7</sup> The keel still further depressed in the direction of the arrow so that the stigma is extruded through the orifice at the apex of the hollow cone.

extent the end of the style also protrudes through the opening (see fig. 270<sup>7</sup>) and comes into contact with the abdomen of the bee which is visiting the flower at the time.

This kind of pump-apparatus appears to be confined to papilionaceous flowers. On the other hand, the mechanism to be described next, which does its work by means of impact, occurs in flowers belonging to the most diverse families. In every case of the kind the movement of the filaments, which results in the transfer of pollen to the body of an insect, resembles the striking of the hammer on a bell, although the cause of the movement is not the same in the different flowers. Sometimes a two-armed lever is set in motion; sometimes there is a sudden recoil of the stamens due to their liberation, as it were, from a vice, and in a third class

of cases the filaments are irritable and on the slightest touch undergo a change of position analogous to the closing up of the leaves of the Sensitive Plant (*Mimosa*; see vol. i. p. 537) when subjected to a like stimulus.

The best known examples of the hammer form of mechanism occur in the genus *Salvia*. In no species of that large genus is it developed to greater perfection than in *Salvia glutinosa*, which we therefore select for illustration. The flowers of this Labiate are set laterally on the stem, and the under-lip serves as landing-stage for the humble-bees to alight on (see fig. 271). If a bee, after alighting, is to obtain the honey which is hidden in the back part of the flower near



Fig. 271.—Transference of pollen to the bodies of insects by means of mechanism of the percussive type.

<sup>1</sup> Part of an inflorescence of *Salvia glutinosa*; the right-hand flower is being visited by a humbly-bee, and the pollen-covered anther is in the act of striking the insect's back. <sup>2</sup> Another part of the same inflorescence with three open flowers in different stages of development: the lower flower on the left-hand side is being visited by a humbly-bee which carries on its back pollen from a younger flower and is rubbing it off on to the deflexed stigma. <sup>3</sup> A stamen of *Salvia glutinosa* with rocking connective. <sup>4</sup> Longitudinal section through a flower of the same plant. The arrow indicates the direction in which humbly-bees advance towards the interior of the flower. <sup>5</sup> Same section; the lower arm of the connective-lever is pushed backward, and in consequence the pollen-covered anther at the end of the other arm of the lever is deflexed.

the ovary, it must advance from the under-lip into the gaping jaws of the flower. It is there that the curious mechanism is set ready. On either side of the entrance is a stamen (see fig. 271<sup>3</sup>) composed of a short, erect, firm, and immovable filament, and an anther borne at the extremity of a much elongated and slightly curved connective which rocks at the top of the filament. The connective is articulated to the filament in such a manner as only to be able to swing in the direction indicated in figs. 271<sup>4</sup> and 271<sup>5</sup>. The part of the stamen which is liable to be set rocking is a curved lever consisting of two arms of unequal length. The upper arm is the longer and terminates in the anther, whilst the under and shorter arm is somewhat thickened and spatulate at its free extremity. When a humbly-bee pushes the lower arm in the direction of the arrow (fig. 271<sup>4</sup>) the upper arm drops (fig. 271<sup>5</sup>).

As the two stamens are close together and the lower arms of the connective practically touch one another, the upper arms fall simultaneously, and anyone observing the phenomenon from the side might think there were only a single rocking anther in the flower. Thus, when a humble-bee, making its way from the landing-stage of the under-lip to the floral receptacle, comes against the pair of short lever-arms barring the entrance, the anthers drop simultaneously upon its back and cover it with pollen (271<sup>1</sup>). We shall show in a subsequent section that bees laden in this manner rub the pollen off on to the deflexed stigmas of the flowers they subsequently visit (271<sup>2</sup>). The hammer-apparatus in the flowers of *Salvia officinalis*, which grows broadcast on the shores of the Mediterranean, only differs from the above in that a little pollen is developed in addition at the end of the lower arm of the lever, and is brushed off on to the head of the insect. The rocking part of the stamen in every species of *Salvia* must be looked upon as an anther with a specially modified connective. The connective is transformed into a long curved lever bearing an anther-lobe at each end. In *Salvia glutinosa* only the lobe at the upper end is polliniferous, whilst at the lower extremity there is a complete absence of pollen. In *Salvia officinalis*, on the other hand, a little pollen develops, as we have seen, in the smaller lobe at the end of the shorter arm also. In the numerous species of which *Salvia pratensis* is a type the filaments are extremely short, and the lower arm of the lever in each case is metamorphosed into a quadrangular flap or valve. The flaps of the two opposite stamens are joined so intimately together that they close the mouth of the flower like a trap-door. Each valve, however, has a little notch in the side adjoining the other, and the two notches coincide so as to form an orifice in the middle of the trap-door. Insects insert their probosces through this hole, and in so doing push the trap-door backwards and upwards. The valves of the trap-door being also the short arms of the lever-apparatus, their ascent is accompanied by the descent of the long arms, each of which bears an anther-lobe full of pollen at its extremity, and in this manner the upper surface of the insect's body is covered with pollen as it sucks the honey.

In the *Lopezias* indigenous to Mexico, the effect of the striking of insects by the anthers is to load, not the upper, but the under surfaces of their bodies with pollen. These plants (*Lopezia coronata*, *L. miniata*, *L. racemosa*) are remarkable for having only a single anther-bearing stamen in each flower. The stamen is wedged in a sterile, petal-like staminode inserted immediately below it; this staminode has its free end fashioned into the shape of a spoon. This spoon-shaped extremity affords the most convenient alighting-place, and the moment an insect settles upon it the staminode suddenly flaps down, whilst at the same instant the stamen concealed within it (being previously in a state of tension) springs up, striking the under surface of the insect's body and covering it with pollen.

The flowers of the Barberry (*Berberis*) have irritable filaments which cause the anthers to strike against insects. There are six stamens arranged in two whorls in each flower; they slope obliquely outwards, and are concealed in the concave



petals which are inserted behind them. Honey is produced in abundance from saffron-coloured swellings on the petals, and is to be found in the interior of the flower sticking to those sides of the filaments which face the ovary. Both hive-bees and humble-bees covet this honey and fasten on to the pendent racemes to obtain it. Often, in the very act of laying hold of a flower, an insect inserts its forelegs into it and touches the stamens; but even if this does not happen, the bases of the stamens are sure to be touched when the insect introduces its proboscis to suck the honey. The slightest touch administered to the lower third of a stamen's length acts as a stimulus, and results in an alteration in the tension of the tissues, and in a sudden backward movement or up-springing of the stamen. The anther is thus caused to strike upwards against the insect, covering its head with pollen, whilst the proboscis and forelegs are also besmeared, though to a less degree.

The transference of pollen to the bodies of insects takes place in the *Opuntia* in the same manner as in the Barberry. The comparatively large flowers of *Opuntia nana*, which grows in Dalmatia and near Sion in the Rhone Valley, &c., open at nine o'clock in the morning when the sky is clear. The fleshy four-lobed stigma may then be seen crowning the thick conical style and forming obviously the most convenient place for insects to alight on. The style rises out of a pit which contains a copious supply of honey, and is surrounded by a large number of erect stamens of different lengths. The dehiscent anthers are charged with pollen of a crumbly consistency; the filaments have the lowest quarter of their length coloured pale yellow and the upper part bright gold. If the golden region of the filament is touched, it curves inwards, forming a semicircular and slightly twisted bow, surmounting the honey-receptacle out of which the style rises. When a bee visits the flower, it settles first on the large stigma, which projects above the anthers, and then tries to clamber down to the honey. During this process contact with the irritable portion of the filaments is inevitable, and the moment it occurs the stamens that are touched bend over the bee and load it with their pollen which is easily detached from the anthers. It is amusing to watch this phenomenon and observe how quickly one after another the filaments bend over the insect, and administer their blows as it crawls down. The bee is not much alarmed by the inflection of the filaments, or by the taps it receives, but suffers itself to be loaded with pollen without making any fuss. It is able to brush it off subsequently and collect it in the "honey-baskets" borne on the tibiæ of its hind-legs. As the inflection of the stamens lasts at least until the insect leaves the flower, a further supply of pollen is sure to be rubbed off when the bee begins to retreat. Usually, when bees leave *Opuntia* flowers, they are dusted all over with the yellow pollen.

Part of the pollen, in the case where the anthers belong to a mechanism of the percussive type, is appressed and affixed to the insect's body, whilst part is brushed off owing to the movements of the creature when it takes its departure from the flower. In this respect the apparatus differs from contrivances of the *explosive* variety, which are adapted to besprinkle or bespatter insects with pollen. The explosion is due to a sudden up-springing of some organ, which may be the style, the filaments

or, as in a few Orchids, the anthers and rostellum. The number of these contrivances is very large, and I must therefore confine myself to an account of the most curious forms, beginning with the case of *Crucianella stylosa*, which grows native in Northern Persia, and is represented in figs. 272 and 274<sup>1</sup>. This plant belongs to the Stellatæ group of Rubiaceæ. Its rose-coloured flowers are conglomerated in terminal heads (274<sup>1</sup>), and scent the air with honey to a considerable distance. If one side of the corolla be removed, the first peculiarities that strike the observer are that the long slender style is twisted into a spiral, and that the thick stigma

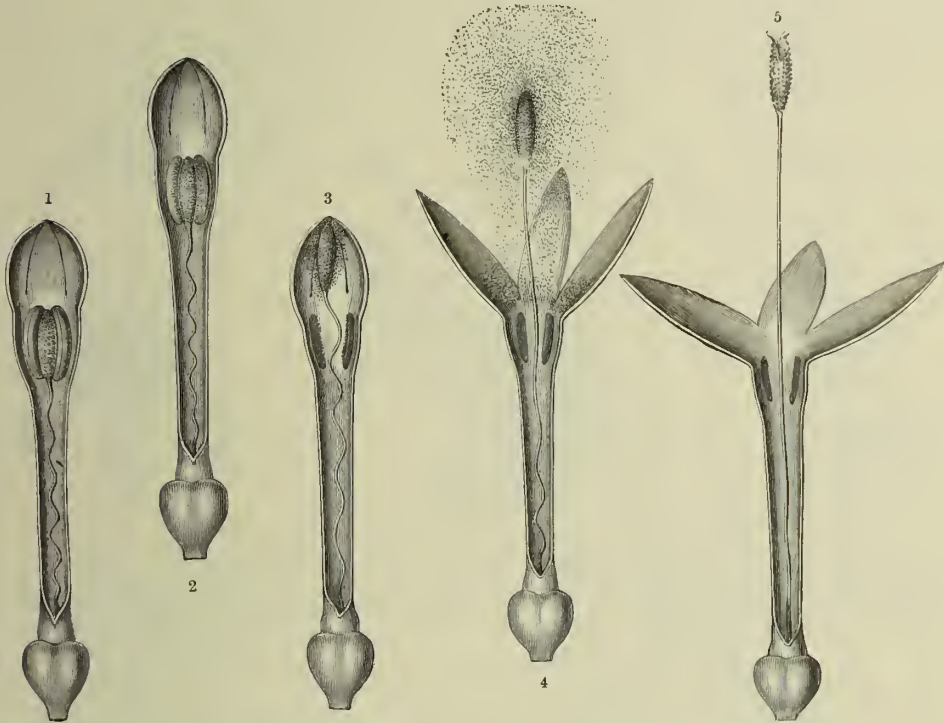


Fig. 272.—Explosive apparatus for the transfer of pollen to the bodies of insects

<sup>1</sup> Longitudinal section through the unopened flower of *Crucianella stylosa*; the papillose stigma wedged between the closed anthers. <sup>2</sup> The same after the dehiscence of the anthers; the pollen deposited on the papillose surface of the stigma.

<sup>3</sup> The stigma covered with pollen has been carried up owing to the elongation of the style until it rests under the dome of the closed flower. <sup>4</sup> The corolla has burst open, and the style, springing up suddenly in consequence, is discharging the pollen from the surface of the stigma. <sup>5</sup> The style projects far beyond the corolla and bears the open two-lipped stigma

which is now first mature and ready to be pollinated. All the figures  $\times 4$ .

at the top of it is wedged between the anthers (see fig. 272<sup>1</sup>). The moment the anthers open the pollen pours out of the loculi and rests upon the papillose surface of the stigma (fig. 272<sup>2</sup>). Soon afterwards the style elongates and its coils relax somewhat, the result being that the stigma, with its coating of pollen, is carried up above the now empty anthers until it comes against the dome-shaped top of the closed corolla where its further ascent is stopped. At this stage of development (fig. 272<sup>3</sup>) the style is in a condition of such extreme tension that the instant the limb of the corolla opens it springs up, scattering a cloud of pollen from the surface of the stigma (fig. 272<sup>4</sup>). In the absence of insects this ejection of

pollen takes place spontaneously; but a sudden opening of the corolla-limb is caused if a small bee or fly chances to touch the top of a closed flower on its way to visit an open one, and the insect is then dusted with pollen from below as is shown in fig. 274<sup>1</sup>. The subsequent events occurring in these flowers will be described later on, and an explanation of fig. 272<sup>5</sup> will then be given.

The species of the genus *Schizanthus*, indigenous to Chili and Peru, one of which—*Schizanthus pinnatus*—is cultivated in our gardens as an ornamental plant, have long been known to possess mechanism for the explosive distribution of pollen. The most conspicuous object in the open flower of any of these plants is a single up-turned speckled lobe, whose function it is to attract insects. Beneath it are two smaller incised lobes which form a sort of keel, affording a convenient place

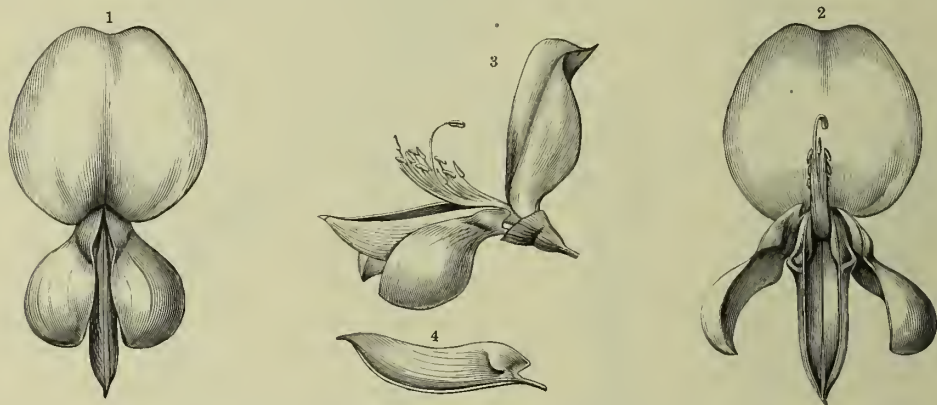


Fig. 273.—Explosive apparatus in a papilionaceous flower.

<sup>1</sup> Flower of *Spartium scoparium* (*Sarothamnus scoparius*) seen from the front, the keel closed. <sup>2</sup> Same flower with the keel open; the stamens previously concealed there together with the style have sprung up. <sup>3</sup> Side view of the same flower after the opening of the keel and springing up of the stamens. <sup>4</sup> One of the two component petals of the keel seen from within.

for insects to alight on. Fixed firmly in the furrow of this keel are two stamens, which are released the moment an insect settles on the keel and introduces its proboscis underneath the vexillary petal above described. The stamens then spring up, and the pollen is scattered out of the anthers.

The occurrence of a similar up-throwing of pollen in the flowers of the Yellow *Corydalis* and a few other species of the same genus (*Corydalis lutea*, *C. ochroleuca*, *C. acaulis*) has been already noted (p. 228) in the account given of the stirrup-shaped lobes on the sides of those flowers. We have only to add that the articulation of the projecting left-hand petal to the two contiguous median petals forming the saddle ceases the moment an insect sprawls upon the saddle and inserts its proboscis underneath the spurred petal. This disconnection has the immediate effect of causing the saddle to drop and the stamens hitherto concealed in the cavity to spring up. The meal-like pollen of *Corydalis* being liberated early, is by that time lying loose upon the anthers, and is ejected upon the under surface of the insect when the stamens are thus suddenly released (cf. figs. 257<sup>3</sup> and 257<sup>4</sup>, p. 226).



The phenomenon of an upward discharge of pollen is also well exhibited in the Melastomaceæ and in many Papilionaceæ of the genera *Astragalus*, *Indigofera*, *Medicago*, and *Phaca*, as also in *Genista*, *Retama*, *Sarothamnus*, *Spartium*, and *Ulex*. We will select *Spartium scoparium*, a plant belonging to the Mediterranean Flora (figured in vol. i. p. 331), as a representative of this group. Figs. 273<sup>1</sup> and 273<sup>2</sup> show the front views of a flower of *Spartium scoparium*, and one



Fig. 274.—Transference of pollen to the bodies of insects by means of explosive apparatus.

<sup>1</sup> *Crucianella stylosa*; the pollen is being discharged from the flowers on to the belly of a hymenopterous insect. <sup>2</sup> *Spartium scoparium*; in the lowest flower the keel is still closed and stretched out horizontally; in the flower next above, the keel is depressed and the stamens have sprung up; the third flower is being visited by a Carpenter Bee (*Xylocopa violacea*), and is ejecting its pollen on to the under surface of the insect's body.

recognizes at once the large upturned standard, the two lateral petals and underneath them the keel composed of a pair of contiguous petals. Near the base of each keel-petal is observed a swelling and a depression (fig. 273<sup>4</sup>), which correspond with portions of the structure of the two wings, so that the latter pair of petals locks with the keel, and every pressure upon the wings from above affects the keel also. A blunt tooth may also be seen near the base of each of the wings (see fig. 273<sup>3</sup>). When the flower is closed the teeth are hidden under the standard; in the open flower they are pressed against the standard, and so keep the wings, and indirectly the keel, in a horizontal position.

In the keel are concealed a style and ten stamens, all in a state of tension like watch-springs. The anthers liberate their pollen very early, and it accumulates in the front part of the keel. When the pulvinate wings, and through them the keel, undergo pressure from above, the blunt teeth which fasten the wings and keel together slip down, and both wings and keel fall with a sudden jerk, whilst the stamens and style lying at the bottom of the keel spring up, throwing the mealy mass of pollen into the air. In nature the object to which the pressure on the wings is due is usually a largish insect, and the result is of course just the same, so that the under surface of the creature's abdomen receives the discharged pollen (fig. 274<sup>2</sup>).

The pollen in these flowers being of floury or powdery consistency, a great cloud of dust is emitted whenever the explosive mechanism is brought into play. The same effect is produced as if the flowers exploded, and several of the plants in question—as, for instance, the various species of the genus *Schizanthus*—are called by gardeners “plants with explosive flowers”. Apparatus for ejecting the whole of an anther's pollen at once in a single coherent mass are of much rarer occurrence. The flowers of a Brazilian shrub named *Posoqueria fragrans*, belonging to the order of Rubiaceæ, and those of a few tropical Orchids are especially remarkable in this respect. The blossom of *Posoqueria* reminds one in many ways of that of the Honeysuckle, exhibiting like the latter a corolla composed of a long horizontal tube and five short limb-segments which are somewhat reflexed when the flower opens. The opening takes place in the evening; the corolla is white, secretes honey at the bottom, and emits at dusk and during the night a pervading scent—all characteristics of a nature to indicate that the flowers are adapted to the visits of Sphingidæ. The abundant honey at the base of the tube can only be reached by the tongues of Sphingidæ; and only these insects, e.g. *Sphinx rustica*, whose proboscis is 15 mm. long, have been seen to visit the flower.

The five anthers are united into an oval knob directed obliquely downwards and containing the loosely-coherent pollen which escaped from the anthers before the expansion of the flower. The filament of the lowest stamen possesses a very considerable elastic tension acting upwards; those of the upper and lateral stamens have a similar tension outwards. The insect's proboscis has only one available point at which to enter the flower, and when in doing so it touches one of the upper stamens at a certain spot the tension of the stamens is released. The lowest stamen springs up with such violence that it hurls the loosely-coherent pollen against the insect's proboscis at an angle of 50° with the tube of the corolla, and with an initial velocity of about 3 mm. per second; at the same time it closes the entrance to the tube. The upper and lateral stamens spring at the same time to the sides, the empty anthers of an upper and a lateral stamen remaining coherent on either side. About twelve hours afterwards the lowest stamen extends itself again and leaves the entrance to the flower open once more. If a hawk-moth, after exploding a flower in the first stage, comes

to one in the stage under consideration, it is repaid for its startling reception in the former case by a rich supply of honey; and in thrusting its pollen-dusted proboscis down to the base of the flower it brings it in contact with the stigma, which stands in the middle of the tube.

The most noteworthy cases of Orchids furnished with expulsive mechanism

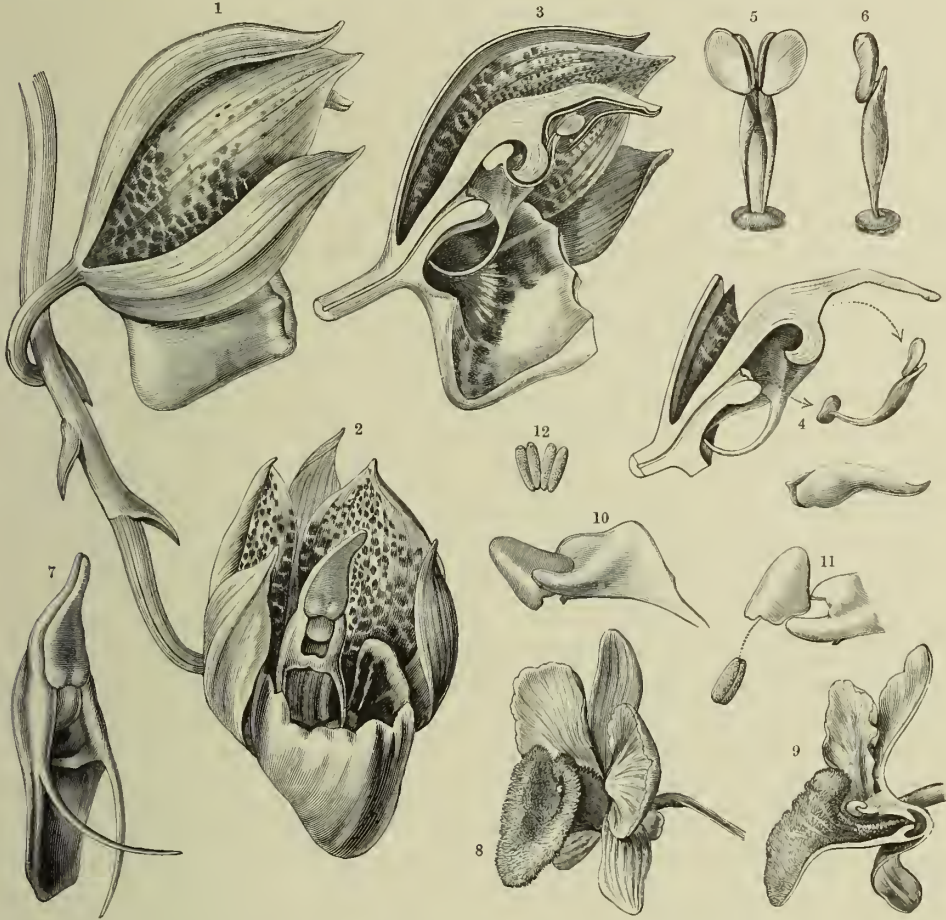


Fig. 275.—Expulsive apparatus in Orchid-flowers: flower of *Catasetum tridentatum*.

<sup>1</sup> Side view. <sup>2</sup> Front view. <sup>3</sup> Longitudinal section through the same; the band connecting the pollen-masses with the viscid disc is stretched like a bow over the protruding rostellum. <sup>4</sup> The pollen-masses and viscid disc are liberated and are being jerked away by the sudden straightening of the connecting-band; the anther-case which hitherto concealed the pollen-masses tumbles away at the same time (below). <sup>5</sup> Front view of pollen-masses, viscid disc, and the band connecting them; the margins of the band somewhat involute. <sup>6</sup> Side view of the same. <sup>7</sup> Column removed from the flower; towards the summit is the anther, below it the elastic connecting-band stretched like a bow; next the stigmatic chamber with its fleshy margins prolonged into two horn-like irritable processes. <sup>8</sup> Flower of *Dendrobium fimbriatum*. <sup>9</sup> The same in longitudinal section. <sup>10</sup> Side view of the hood-like anther at the end of the column. <sup>11</sup> The anther jerking back and ejecting the pollen-masses. <sup>12</sup> Pollen-masses of *Dendrobium fimbriatum*. <sup>10</sup>, <sup>11</sup>, <sup>12</sup>  $\times 5$ ; the rest natural size

are those of the genera *Catasetum* and *Dendrobium*. *Catasetum* will need a somewhat detailed account, for the reason that in this genus the process of expulsion ensues upon an external stimulus which does not act upon the mechanism in question direct, but is transmitted through a special organ. The column in the flower of *Catasetum* (see figs 275<sup>1</sup> and 275<sup>2</sup>), as in many other Orchids, rises



up over a hollow labellum. Near the apex of the column is the anther, and lower down the rostellum, whilst below the rostellum the column is deeply excavated. The edges of this pit are fleshy, and are prolonged into two curious processes resembling a pair of horns. These processes are curved and tapering, and are inclined obliquely forwards and downwards. In most species, including *Catasetum tridentatum* (here represented), the horns (or antennæ, as they are sometimes called) cross one another diagonally (see fig. 275<sup>7</sup>). Each horn, originally a ribbon-like lobe, is rolled up lengthwise so as to form a tapering tube. The substance of both horns passes without any definite line of demarcation into the tissue of the rostellum above. Although this tissue has been examined with the greatest care, nothing special has been found in it to account for the extraordinary irritability which it exhibits. It has been ascertained by experiment that any pressure on the lower extremity of the horn acts as a stimulus, and that this stimulus is at once transmitted upwards through the cells of the tissue to the part of the rostellum which forms the viscid disc. The slightest touch applied to the tip of one of the horns is instantly followed by the rupture of the tissue which has hitherto retained the viscid disc in position, and by the consequent liberation of that portion of the rostellum. The viscid disc had, however, in its turn served to keep a curved elastic band which attaches the disc to the pollinia on the stretch, and in its proper position (fig. 275<sup>3</sup>), so that when the disc is set free the band flies up and straightens itself up with a jerk. The viscid disc and the pollinia are torn from their recesses by the recoil of the band, and are carried with it in an ample curve away from the column, which till then has served as their common base (fig. 275<sup>4</sup>). During its flight the viscid disc goes first, and it naturally, by sticking to some object in the way, brings the pollen-masses to a standstill. From the time of its being shot off, the band connecting the disc and the pollinia is quite straight (see figs. 275<sup>5</sup> and 275<sup>6</sup>).

The expulsive apparatus exhibited by most species of *Dendrobium* is altogether different. In the species selected for illustration—viz. *Dendrobium fimbriatum* (figs. 275<sup>8</sup> and 275<sup>9</sup>)—the column is capped by an anther in shape like a bell. The anther is septate, and contains in its loculi pollen-masses, which since they are unconnected with any viscid disc, are therefore liable to fall out of the anther in certain positions of the latter. The anther is borne by a slender subulate filament, to the extremity of which it is articulated in such a manner that a gentle push is sufficient to set it rocking. When the flower first opens, and before it has yet been exposed to any contact, the bell-shaped anther rests mouth downwards on a notch at the top of the column, and is held in that position by two tooth-like processes to the right and left of the notch (see fig. 275<sup>10</sup>). A push administered from the front displaces the anther and causes it to fly back, whilst the pollinia contained in it are simultaneously expelled (see fig. 275<sup>11</sup>). The pollinia being unfurnished with viscid discs (fig. 275<sup>12</sup>), it is not quite evident how the insects which supply the necessary stimulus on their visits to the flowers get loaded with the pollen. There is, however, every probability that the expulsion

is followed by a transference of the pollen to the bodies of the insects. Unfortunately we do not know of any observations having been made of the visits of insects to plants of this species in the wild state. Such observations might enable us to come to a sure conclusion on the subject, but so far all our results have been derived from flowers reared in hot-houses.

Next to the expulsive variety of mechanism comes the *sprinkling* variety. Pollen transferred by this kind of apparatus is always of mealy or powdery consistency, and is shaken out of the loculi where it is produced. Three modifications of this apparatus may be distinguished, viz.:—the sugar-tongs modification; that in which the anthers dehisce by terminal pores; and that in which the anthers are united into cones. In contrivances of the first kind, the filaments are like the arms of a pair of sugar-tongs, and the anthers borne by them are, when in the dehiscent condition, in the form of spoon-shaped receptacles or recesses, with the concave sides facing one another. Pollen of mealy consistency would not stay in open, upright spoons of the kind were it not for a special contrivance. In order to picture the state of things it is best to think of the action of a pair of sugar-tongs in which the end of each arm is fashioned into a spoon. When the tongs are closed the concave surfaces of the spoons are brought together, and form a receptacle in which sugar can be retained in the form of little solid bits, and even in the form of fine powder if the parts of the tongs fit well. The moment the two arms of the tongs are separated the contents held by the spoons drop down, and if in the condition of powder they must inevitably bepowder any object that may happen to be underneath. Now, this is just what occurs in connection with the sprinkling apparatus in the flowers of a large number of Acanthaceæ, Rhinanthaceæ, and Orobanchaceæ. Beneath the protective covering of the floral envelopes—most commonly under the upper lip of a bilabiate corolla—are found the stamens arranged two and two, with the anthers of each pair closed together like the two valves of a leguminous pod. They are kept in this position by the stiff staminal filaments, and the margins of the valves fit one another so exactly that not a single pollen-cell from the mass of floury pollen contained between them can fall out unless the structure is subjected to some particular shock. In some cases each pair of opposite valves is furnished with matted hairs which join the upper edges together. The form is then like that of a mussel-shell, and only the free margins can open. The moment the valves separate in the least, whether they are joined together at one part or not, the pollen spills out in accordance with the law of gravity. The direction of its fall is often determined by delicate hairs fringing the margin of the anther, the object being to prevent waste. The separation of the valves is caused by insects—and in tropical regions probably by humming-birds as well—when they press into the jaws of the flowers in search of the honey stored in the back-ground. In doing so the proboscis (or beak) is either pushed right between the valves, or it strikes against certain special processes with which the valves are furnished, or else the tense filaments bearing the valves are forced

asunder. The first is what occurs in *Bartsia alpina*. In the flowers of this plant the entrance is much narrowed, owing to the curving up of the limb of the under-lip, and close behind the entrance are found the anther-valves, which are comparatively large, and are edged at the top with matted hairs. Before an insect can reach the honey on the floral receptacle it has to force apart the lower edges of these valves, thus letting the pollen fall out upon itself. In the flowers of the Yellow-Rattle and Toothwort (*Rhinanthus*, *Lathræa*), the entrance is still more exactly defined, and the insect cannot deviate a hair's-breadth from it without sustaining injury. The filaments bearing the valves, which in this case are posted

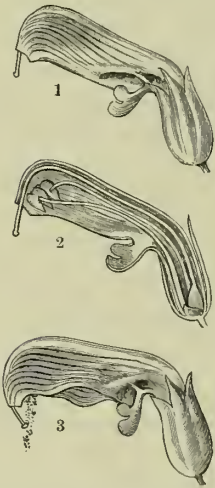


Fig. 276.—*Pedicularis recutita*.

<sup>1</sup> Entire flower. <sup>2</sup> Longitudinal section of the same. <sup>3</sup> Pollen falling out in consequence of the inclination of the helmet-shaped part of the corolla.  $\times 3$ .

in the middle of the entrance, are beset with rigid prickles liable to injure an insect's delicate proboscis, and the only safe path to the receptacle lies between the ciliated anther-valves, which part asunder on being pushed with any moderate force (see figs. 277 <sup>4, 5, 6</sup>). In *Clandestina*, *Trixago*, and several other *Rhinanthaceæ*, the filaments are not furnished with prickles, but each anther bears a little downwardly-directed process which is pushed on one side by an insect entering the flower. The corresponding anthers are parted by the displacement of the processes, and the floury pollen is sprinkled upon the head and back of the intruder. In flowers of the Lousewort genus,—*Pedicularis asplenifolia*, *P. rostrata*, and many species allied to them—the anthers are hidden under the arch of the upper lip, and it is impossible for insects to come into direct contact with them. The path of the insects here lies somewhat deeper between the filaments, which they force apart, causing thereby a corresponding change in the position of all the different parts of the flower. In consequence the anthers

also move asunder, and let fall the floury pollen hitherto wedged between them. A somewhat different mechanism is exhibited by several species of the genus *Pedicularis*, which may be represented by the common alpine *Pedicularis recutita* (fig. 276). The anthers in the flowers of this plant are borne on elastic filaments, and are regularly squeezed between the lateral walls of the helmet-shaped (*galeate*) upper lip. No separation of the valves is possible unless the galeate lip expands and becomes laterally inflated. This is brought about in a very curious manner. When a humble-bee alights it seizes the projecting upper lip and bends it down through an angle of about  $30^\circ$ , this action being facilitated by the presence of strong ribs at the base of the helmet on either side of the throat of the corolla which act like levers, and communicate their motion to the entire upper lip. In consequence of the inclination of the upper lip, the sides of the helmet, which up to this time are tightly stretched, bulge out laterally; secondly, the filaments bend in the same sense as the bulging sides of the helmet; and thirdly, the anthers themselves come apart pouring the



pollen-dust on to the insect's back. In order that this complicated machinery may do its work successfully, the insect must insert its proboscis at a certain definite spot through a little groove in the under lip, and for this reason all other spots where entrance into the flower might be attempted are barricaded. The margin of the upper lip, for instance, is thickly furnished with short-pointed prickles which the insects take care not to touch (*cf.* figs. 276<sup>1, 2, 3</sup>).

The chief points of difference between the kinds of sprinkling apparatus hitherto described and that which occurs in *Acanthus* flowers (*Acanthus longifolius*, *A. mollis*, *A. spinosus*; see figs. 277<sup>1, 2, 3</sup>) are that in the latter the anthers

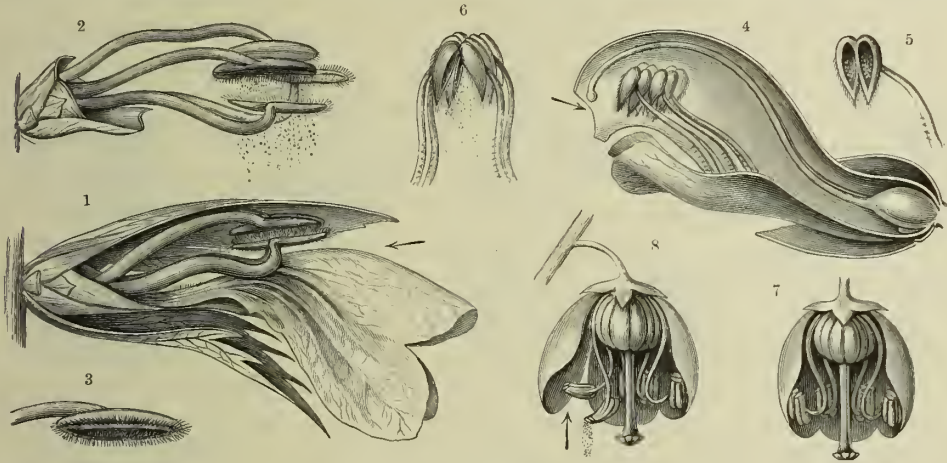


Fig. 277.—Sprinkling apparatus.

<sup>1</sup> Flower of *Acanthus longifolius* with some of the petals cut away. <sup>2</sup> Stamens of *Acanthus* illustrating the sugar-tongs principle; the anthers parted so as to let fall the pollen. <sup>3</sup> Single anther of *Acanthus* showing fringe. <sup>4</sup> Longitudinal section through the flower of *Rhinanthus angustifolius*. <sup>5</sup> Stamen from the same. <sup>6</sup> The four stamens of *Rhinanthus* seen from the entrance to flower; the anthers in contact at the top, parted below; the pollen falling out. <sup>7</sup> Flower of *Pyrola secunda* with some of the petals and stamens cut away. <sup>8</sup> The same; the anther is capsizing owing to the displacement of the petal which has hitherto kept it in position, and pollen is being sifted through the pores. The arrow in figs. 1, 4 and 8 indicates the direction in which an insect enters the flower. 1, 2 natural size; the rest  $\times 2$  to 5.

are unilocular instead of bilocular, and that the loculus resembles a long narrow niche rather than the valve of a mussel-shell. Each niche is edged with close short down, a provision which conduces materially to effective closure when the two anthers are in contact. The filaments look as if they were made of ivory; they are unusually strong, and are not so easily pushed asunder. Sturdy humble-bees of large size alone are able to displace these filaments, and the result of their doing so is to part the anthers and cause a shower of floury pollen to descend upon their bodies.

A form of sprinkling apparatus very different from the sugar-tongs variety, with its spoon-shaped anther lobes, is exhibited where the anthers act like pepper-casters. Contrivances of this type occur chiefly in bell-shaped blossoms which are either pendent or nodding. The anthers are furnished at or near their free extremity with two little pores, and are so placed inside the bells as to have the holes facing downwards at the moment when the pollen is to be scattered. The

pollen is of a floury consistency and is tightly compressed in the anthers, but it is sifted out intermittently, a little at a time, somewhat as powdered sugar is shaken through the holes of a castor. In some cases the anthers are suspended inside the bells with their pores downwards from the very commencement, as, for example, in the flowers of the Snowflake (*Leucojum vernum*) and those of the Cowberry (*Vaccinium Vitis-idaea*); but in others the elastic filaments are reflexed and hold the anthers at first with their pores upwards, facing the receptacle of the pendent flower. In order that the pollen may fall out of this class of anthers (with pores directed upwards), they must be turned upside down. This inversion is effected by insects, and as an example we will describe how it occurs in a Winter-green (*Pyrola secunda*). The filaments are curved into the shape of the letter **S** and are in a high state of tension, and the anthers borne by them are held in position, with their pores directed upwards, by the pressure of the petals (see fig. 277<sup>7</sup>). When an insect visits the bell it displaces the petals with the result that the filaments straighten out and the anthers are inverted (fig. 277<sup>8</sup>). In a large number of instances the anthers are furnished with special appendages against which insects are sure to strike when they enter the flower, whereupon a little pollen invariably pours out. The Snowdrop (*Galanthus*) has simple rigid points depending from the free extremities of the anthers and standing in the way of insects, and so also have *Cyclamen*, *Ramondia*, and many other plants belonging to widely-different families. The Strawberry-tree (*Arbutus*) and the Bearberry (*Arctostaphylos*; cf. fig. 263<sup>1</sup> p. 240) have two little horns projecting from the back of each anther, against which insects knock in their quest for honey, the result being that the whole anther is shaken and scatters pollen through its pores.

Anthers which dehisce by pores and act in the manner above described are usually associated with actinomorphic (*i.e.* radially symmetrical) and either pendent or nodding flowers, and all the cases we have examined hitherto have in fact been of pendent or nodding bells of perfectly regular conformation. Of the few zygomorphic flowers (*i.e.* symmetrical about one plane only) furnished with anthers of the kind I can only refer briefly to the Calceolariæ and Melastomaceæ. In these plants the anthers rest on short filaments, and are easily set rocking like those of *Salvia*. But whereas in the flowers of *Salvia* the anthers dehisce longitudinally and contain pollen of viscid consistency, those of the Calceolariæ and Melastomaceæ open by pores, whilst the pollen contained in them is of mealy or powdery consistency. The anthers are set swinging by insects knocking against them, and the pores being thus lowered the pollen comes tumbling out on to the bodies of the intruders.

The third form of sprinkling apparatus consists of a whorl of stiff stamens grouped together so as to form a hollow cone. The anther belonging to each stamen is composed of two lobes which open by longitudinal fissures and after dehiscence are simply open niches. The pollen is in the form of meal or powder, and in order to prevent it from falling out of the niches before the right time a special contrivance is necessary to keep them closed. This result is attained by

two different methods. According to one method the anther-lobes are pressed firmly against the style round which they stand in a small circle; according to the other the lobes of adjacent anthers face one another and are closed as tightly together as were the anthers of the sugar-tongs-like stamens already described. The first arrangement occurs in *Soldanella* (see figs. 278<sup>1, 2, 3</sup>), the latter in many species of *Erica* and of Boragineæ (see figs. 278<sup>4, 5, 6, 7, 8, 9, 10</sup>). In both cases the cone is composed of four or five lanceolate anthers, and the pollen is concealed in eight or ten long narrow loculi which part and let their contents fall if the cone is displaced to the slightest extent. If an insect touches the cone anywhere, as it must do to insert its proboscis, it dislocates the closely-fitting parts and causes a little shower

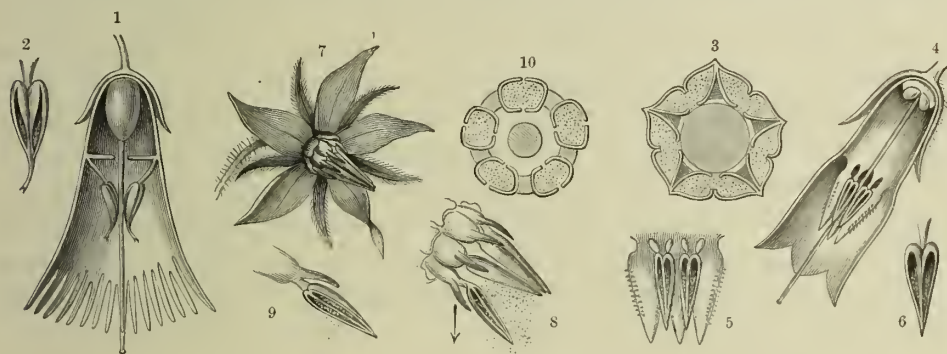


Fig. 278.—Sprinkling apparatus.

<sup>1</sup> Longitudinal section through a flower of *Soldanella alpina*. <sup>2</sup> Stamen from the same seen from that side which is in contact with the style. <sup>3</sup> Diagram of transverse section through the style and the five anthers adherent to it; the lightly shaded part is the style, the darker shaded portions are the connectives, the dotted portions are the pollen. <sup>4</sup> Longitudinal section through a flower of *Symphytum officinale*. <sup>5</sup> Two stamens and three scales of same beset with prickles. <sup>6</sup> Single stamen of *Symphytum*. <sup>7</sup> Flower of *Borago officinalis*. <sup>8</sup> Cone of anthers from the same with one of the stamens bent down in the direction of the arrow, and a little pollen escaping in consequence. <sup>9</sup> Stamen with tooth-like handle on its filament. <sup>10</sup> Diagram of transverse section of the style and anthers of *Borago*; the shaded portions are the style and the connectives of the five anthers, the dotted portion is the pollen. <sup>7</sup> natural size; the rest of the figures  $\times 2$  to  $5$ .

of pollen to descend upon itself. Usually very small quantities of pollen fall at a time. As soon as the proboscis is withdrawn the anthers are replaced in virtue of their elastic filaments, and the same process may be repeated again and again. The insects break into the flowers at various spots; in Heaths (*Erica*) the proboscis is usually introduced through the apex of the cone of anthers, in Borage (*Borago officinalis*; see fig. 278<sup>7</sup>) at its base. The latter plant is visited by hive- and humble-bees which, alighting on the nodding flowers from below, fasten on with their fore-legs, so that their head and proboscis is brought on to a level with the base of the cone, whilst the hind part of the body is arched under its apex. The insect holds on in this position by a peculiar tooth-like appendage of the filament (see fig. 278<sup>9</sup>), and with this as a handle pulls the anther of that stamen away from the rest, causing a break in the cone out of which the pollen falls on to the abdomen of the insect as it sucks the honey. In the flowers of several Boragineæ—Comfrey (*Symphytum*) and *Cerinthe*, for example—there are peculiar scales, furnished with sharp prickles, alternating with the anthers (see figs. 278<sup>4, 5, 6</sup>), and placed in such a position that insects are afraid to insert their



probosces except at the apex of the cone of anthers, and in consequence the head alone and not the abdomen is, in this case, besprinkled with pollen. In *Soldanella* (figs. 278<sup>1</sup> and 278<sup>2</sup>) the apex of each anther is produced into two little processes. Insects come against them as they enter the flower, with the result that pollen is scattered out of the anthers. Several of the wonderful contrivances which were described on p. 271 as occurring in connection with stamens fashioned like sugar-tongs are also present where the conical arrangement of anthers prevails; and we need not, therefore, discuss the latter at greater length. The only case left requiring special attention is that of the Violet and Pansy (*Viola*, fig. 279<sup>1</sup>). Unlike the foregoing, the flower in this case is zygomorphic and has its mouth directed sideways, and moreover, the manner in which the anther-cavities, which are full of floury pollen, are moved by insects is peculiar. The cone of anthers is set over the lowest petal, which is prolonged at the back into a spur containing honey. In order to suck the honey an insect must push under the cone and run its proboscis along the channel of the spurred petal. But here it encounters the thickened extremity of the hooked and deflexed style, which it cannot avoid touching and shifting a little. The five stamens forming the cone are closely adherent to the style, so that any displacement of the latter affects them also, and the moment this happens the proboscis of the intruding insect is besprinkled with pollen from the dislocated cone of anthers.

#### DEPOSITION OF POLLEN.

The pollen which has been taken from one flower has to be deposited in another by honey-sucking insects and birds. How, when, and where the deposition occurs is of great importance, as the transference is in reality the first stage in the series of events leading to fertilization. The stigma is the destination of the pollen, and the right moment for deposition is as soon as the stigma is able to hold fast the pollen which is brought to it. If the pollen is not deposited on the stigma but on some other part of the flower, or if the stigma be dry and shrivelled, and not able to retain the pollen when deposited on it, it is as much wasted as if it had fallen on to the ground or into the water. Hence not only the time and place of deposition, but also the state of the stigma determine exactly the conditions for the success of the transference of the pollen.

If the pollen is scattered on the back of the insect the stigma must come into contact with its back; if it has adhered to the proboscis, the insect must stroke the stigma of the newly-visited flower with its proboscis; if the under surface of its body is covered with pollen, then the stigma will be placed at the bottom of the entrance to the flower, so that the insect must stroke it with its belly. Obviously, then, an insect, whether abstracting or depositing pollen, will follow approximately the same course in the flower, and that position of the anthers most suitable for the shedding of the pollen will, on the whole, be the position most suitable for the stigma to assume in receiving pollen. It might, therefore, have seemed more natural

to describe the two processes of abstraction and deposition of pollen together. Both have already been referred to, but a thorough description would have greatly encroached on the account of the transference of the pollen by animals reserved till now, and so it seems more natural to treat the deposition of pollen more particularly here, while connecting it with the processes described above as occasion requires.

In the last chapter, when describing the change of position of anthers and stigmas, it was especially noted that in the flower of the Grass of Parnassus (*Parnassia*; see fig. 267<sup>4</sup> p. 249) one anther after another placed itself in the centre of the flower, because the road to the honey ran through that part, and the sucking-insects were therefore obliged to remove the pollen from the anther standing in their way. But each anther in turn, as it stands in the centre, covers the stigma which surmounts the egg-shaped ovary, and as long as this is the case, the pollen from another flower cannot be deposited there. It is necessary that the last anther of the series, after giving up its pollen, should move out of the way in order that the stigma may be accessible. This actually occurs; the stigma alone is now to be seen in the place where the five anthers have successively appeared, and when other insects come to suck up the honey, the pollen they bring with them from other flowers is deposited on the stigma. The same sort of thing happens in *Funkia*, *Centranthus* and *Impatiens*. In the flowers of *Impatiens*, the anthers form a kind of cap which covers the stigma so as to hide it completely when the flower first opens. Only when the cap becomes loose and falls off is the stigma exposed, standing in the place formerly occupied by the anthers. In these cases the position taken up by the stigma at the commencement of flowering is not usually altered, so that it meets the pollen-laden insect in the exact place where the anthers formerly stood. In order to attain this end, however, the styles of most Saxifrages (e.g. *Saxifraga bryoides*, *cuneifolia*, *Gewm*, *rotundifolia*, *stellaris*) as well as the stigmas of many Gentians, and especially those in the revolver-flowers of the Caryophyllaceæ undergo an alteration of position. Originally, the stigmas of these flowers were placed together in the centre, and the pollen-bearing anthers stood in a circle round them; but, after the anthers have fallen and their filaments have shrivelled up, the style splits, that is to say, the stigmas separate from one another and diverge, taking up the position formerly held by the anthers when liberating their pollen.

The styles of Labiatæ undergo still more marked movements, as, for instance, in the Sage (*Salvia glutinosa*), a representative of this order. When the flower first opens only the end of the style projects as a simple point from the edge of the upper lip (see figs. 271<sup>1</sup> and 271<sup>2</sup>, p. 262, the right-hand flowers). In this stage the humble-bees, entering the flowers, only carry off pollen, and do not touch the top of the style. Later, the style bends down like a bow, and its branches, at first folded together into a single point, separate and place themselves in front of the entrance to the flower, so that the approaching visitors—the humble-bees—must leave on them the pollen they have brought from other and younger flowers (see

fig. 271<sup>2</sup>, left-hand flowers). A very noticeable change of position of stigmas and anthers is also observed in flowers of the *Gladiolus*, the Hellebore (*Helleborus*), the narrow-leaved Willow-herb (*Epilobium angustifolium*), various species of the genus Honeysuckle (*Lonicera alpigena*, *nigra*, *Xylosteum*, &c.), also in the Figwort (*Scrophularia*), species of the genus *Penstemon* and *Cobæa*, and finally in numerous Solanaceæ, as, for example, in the Deadly Nightshade (*Atropa*), the Henbane (*Hyoscyamus*), *Scopolia*, and the Mandrake (*Mandragora*). Looking into the newly-opened flower of the Mandrake (see fig. 279<sup>8</sup>) we see the spherical, sticky stigma close below the entrance and exactly in the centre. The anthers, surrounding it in a circle, are still unopened and placed against the inner wall of the corolla. Since the mouth of the flower at this time is only slightly open, the stamens are scarcely seen. Two days later the appearance of the same flower is greatly altered. The style, bearing the stigma (now pollinated), has bent sideways and impinges on the inner wall of the corolla, the anthers are pushed towards the middle of the now widely-opened mouth, are covered with pollen, and have thus changed places with the stigma (see fig. 279<sup>9</sup>). In the flowers composing the umbels and capitula of many Umbellifers, Scabiouises, and Composites, the anthers and stigmas may be said to change places in a certain sense, since the stigmas do not mature until the neighbouring stamens have shrivelled up, or their anthers have fallen off. In the heads of many Dipsacæ (*Cephalaria*, *Succisa*), and the head-like umbels of the *Eryngium*, at first only pollen-covered anthers are seen in all the flowers, and later only the stigma-bearing styles. The insects carry the pollen away in masses from these inflorescences, so it is obvious that the deposition must occur in the same manner, *i.e.* that an insect smothered in pollen, alighting on an inflorescence with numerous stigma-bearing styles, and indulging in a series of lively gyrations attaches its load in a few seconds to dozens of the sticky stigmas.

It is hardly necessary to state in detail that the small-pointed thorns, stiff bristles, and other similar structures by which insects are shown the way into the flower have the same significance for the deposition of pollen on the stigma as for its removal from the anthers, and we can now merely refer to the descriptions on pp. 250, 271, and 275. Only one other contrivance especially connected with the deposition of pollen on the stigma, which acts as a remarkable sign-post, need be mentioned here. In the flowers of many Cruciferae, *e.g.* those of *Kernera saxatilis*, whose first and last stages of development are shown in figs. 267<sup>8</sup> and 267<sup>10</sup>, p. 249, the petals at the time of opening are still small, stand erect, or are even somewhat inclined inwards, almost touching the large stigma which nearly fills up the entrance to the flower. Insects wishing to suck the honey at the base of the flower are obliged by this position of the petals to push their probosces down close by the stigma. Should the proboscis have been loaded with pollen in other flowers, this will be inevitably deposited on the stigma. Later, when the stigma is withered, and the floral-leaves have enlarged, the whole flower becomes inflated, the floral-leaves becoming concave inwardly, the pollen-covered anthers become visible and accessible; and now when an insect directs its proboscis to the base it no longer touches



the stigma, but brushes off the pollen from the anthers. The same arrangement is repeated with but little deviation in the flowers of the Asarabacca (*Asarum*). The opening of the perianth in this flower begins with the appearance of three fissures between the three perianth-lobes, and these serve as entrance-gates for the small flies seeking access to the interior of the flower (see fig. 279<sup>12</sup>). The stigmas which are to be pollinated are close below the three fissures, and the insects using



Fig. 279.—Arrangements for the Retention of the deposited Pollen.

- <sup>1</sup> Flower of the Violet (*Viola odorata*); part of the corolla cut away. <sup>2</sup> Capitulate end of the style of this flower seen from underneath. <sup>3</sup> Pistil of the Violet surrounded by the cone of anthers; pollen is deposited on the small lip of the capitulate stigma by the proboscis passing in the direction of the arrow. <sup>4</sup> Stigma of the Narcissus (*Narcissus poeticus*) with finely toothed margin. <sup>5</sup> Stigma of Gladiolus (*Gladiolus segetum*) with ciliated edges. <sup>6</sup> Pistil of *Sarracenia purpurea*; the ovary surrounded by the stamens. <sup>7</sup> Funnel-shaped stigma of the Crocus (*Crocus sativus*); one of the three stigmas only remaining. <sup>8</sup> Flower of the Mandrake (*Mandragora vernalis*) in the first stage of blossoming. <sup>9</sup> The same in the later stage of blossoming. Part of the corolla and calyx cut away. <sup>10</sup> Flower of the Sundew (*Drosera longifolia*) seen from above. <sup>11</sup> Part of the sticky papillose stigma of the Sundew. <sup>12</sup> Flower of the Asarabacca (*Asarum europaeum*) in the first stage of blossoming. <sup>13</sup> The same flower at a later stage. <sup>14</sup> Stigma of *Roemeria*. <sup>15</sup> Stigma of *Opuntia nana*. <sup>16</sup> Stigma of *Thunbergia grandiflora*; pollen is deposited on the lower lip by a proboscis passing in the direction of the arrow. <sup>17</sup> Flower of *Azalea procumbens*; portions of the calyx and corolla cut away. <sup>18</sup> Pistil of the Opium Poppy (*Papaver somniferum*). <sup>6</sup> and <sup>18</sup> natural size; the others somewhat enlarged.

them as entrance-gates must of necessity pass over the stigmas. If they come laden with pollen from an older flower they cannot avoid leaving a portion behind on the stigmas. Later, when the stigmas are pollinated, the three perianth-lobes separate at the tips also, where they have hitherto been joined together (see fig. 279<sup>13</sup>). It is then no longer necessary that the insects should be shown the way to the stigmas.

No less important than the position of the stigma and its relation to the rest of

the flower is its capacity for retaining the pollen brought to it. As might be expected, flowers which are visited by insects agree but slightly in this respect with those which are wind-pollinated. In all the instances where the pollen collected by insects or birds has to be brushed off in adhesive crumbling masses, delicate feathery stigmas, such as those of Grasses and many other plants which receive powdery pollen by wind agency, would be of no use; but to the former, stigmas possessing projecting edges, bands, and lobes, on which the insects as they pass must leave their pollen, are better adapted. Usually close to the projecting edge there is a depression which is filled with the deposited pollen. Thus, for example, the style of *Thunbergia* (see fig. 279<sup>16</sup>) ends in a funnel-shaped stigma whose edge projects on one side like a shovel. When an insect strikes against this stigma on entering, the pollen is received by this shovel and is at once deposited in the funnel-shaped

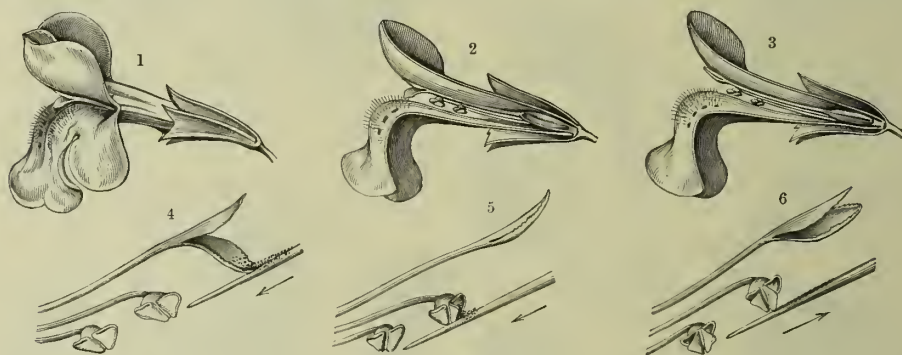


Fig. 280.—Deposition of the Pollen.

<sup>1</sup> Flower of the Monkey Flower (*Mimulus luteus*). <sup>2</sup> The same flower cut in half lengthwise with open stigma. <sup>3</sup> The same flower with closed stigma. <sup>4</sup> Pollen is deposited on the lower lip of the stigma by a proboscis passing in the direction of the arrow. <sup>5</sup> The stigma has closed in consequence of the stimulation: the proboscis passing in the direction of the arrow opens the closed anthers and loads itself with pollen. <sup>6</sup> The lower lobe of the stigma is only slightly raised so that it does not come into contact with the proboscis which is being withdrawn in the direction of the arrow, and consequently the pollen adhering to it does not reach the stigma. 1, 2, and 3 natural size; the others somewhat enlarged.

depression. Insects which push their probosces into the flowers of the Violet (*Viola*) inevitably strike against a little flap projecting from the lower side of the capitate stigma (see figs. 279<sup>1, 2, 3</sup>), and when the proboscis is covered with pollen this is left adhering to the inner side of the lobe. When the insect withdraws its proboscis the lobe is pressed back against the stigmatic head, and thus the recently received pollen is pushed into its cavity. The flowers of Irises possess stigmas with the shape and colour of petals. They are bilabiate at their free end (see figs. 265<sup>1</sup> and 265<sup>2</sup>, p. 246). The upper lip of the stigma is curved, fairly large, and split into two points, the lower lip is thin and forms a narrow membraneous lobe spread out transversely. The path traversed by the humble-bee in obtaining the honey passes under one of the bilabiate stigmas, and when it comes laden with pollen from another flower it pushes down the thin flap of the lower lip, so that the pollen is brushed from its back and deposited between the two lips. Many Scrophulariaceæ and Lentibulariaceæ (*Catalpa*, *Mimulus*, *Rehmannia*, *Torenia*, and *Utricularia*), of which the Monkey-flower (*Mimulus luteus*, see figs. 280<sup>1, 2, 3</sup>), may serve as a type,



have bilabiate stigmas which exhibit sensitive movements. When the pollen is deposited by an insect on the lower lip of the stigma, which stands in its way as it enters (280<sup>4</sup>), the two lips immediately close together like the leaves of a book (280<sup>5</sup>), and thus the pollen is carried to that part of the stigma where it undergoes further development. When the insect withdraws its proboscis there is no chance of the pollen which it is taking from the anthers getting into the interior of the stigma, since the stigma is still shut up and no longer stands in the way of the insect (280<sup>6</sup>). The stigma of *Mimulus luteus* remains closed after being stimulated with a needle for about five minutes; when it again opens, the lower lip resuming its former position, it may be again closed if further stimulated. In other species of the genus, as also in *Martynia* and *Catalpa*, the same phenomenon is observable. None of the previously-mentioned plants appear to keep their stigmas closed more than two minutes. This repeated opening of the stigma is very important in case the first insect visiting the flower should have brought no pollen with it. Since the stigma opens again it has apparently some expectation of a second visit. Should this also be unsuccessful it may open a third time. The opening and closing usually continue until at length an insect deposits pollen on the stigma. When this happens the stigma, though opening yet again for a brief period, remains permanently closed so soon as the influence of the pollen is felt.

The contrivances described above are based on the fact that the pollen stroked off the visiting insects by the projecting edges, bands, and lobes, is conducted from them to the portion of the stigma adapted to receive it. To this first group of contrivances for retaining pollen may be added another where the insect on entering into the base of the flower leaves the pollen it has brought on the papillose, superficial cells of the stigma. This occurs, for example, in the flowers of *Malvaceæ* and *Caryophyllaceæ*, the styles of which are studded with long tube-like papillæ; they act like brushes. In the flowers of the Rock-rose (*Helianthemum*), and in those of the Day-Lily (*Heimerocallis*), long papillæ are grouped paint-brush-wise on the capitate stigma, but most frequently the trimming of very numerous long and crowded papillæ has the appearance of velvet, and such stigmas are termed "velvety" by descriptive botanists. The genera *Erythræa*, *Daphne*, and *Hibiscus* may be mentioned as well-known plants with velvety stigmas. In many plants the stigmatic papillæ are but slightly prominent, the surface appearing rough, irregular, or granulated. If the flowers are crowded, and the deposition of pollen occurs simultaneously on numerous stigmas, these are usually linear or only beset with papillæ on one side, as in *Cephalaria*, or clothed all over, as in *Armeria*, but always so formed and placed that the insect moving over the flower-head may rub off its pollen as easily and quickly as possible on to the stigmas. In those plants where the stigma rising in the middle of an erect, shallow flower is used as a resting-place by the insect, either the whole surface is thickly beset with papillæ (e.g. in *Roemeria*, fig. 279<sup>14</sup>), or they are arranged in the form of rows distributed in radial lines, as in the Poppy (*Papaver*, fig. 279<sup>18</sup>). It frequently happens that the papillæ only border the edge of the stigma, resembling eyelashes on an eyelid,



or the teeth of a comb. This is particularly the case if the stigma is lobed, the lobes being fairly large and spoon-shaped, cup-shaped, or like a funnel, and if the insect on entering only touches the edge of the stigmatic lobes with the pollen-laden part of its body. This is the case, for example, in the flowers of many *Gentians*,



Fig. 281.—Evening Primrose (*Oenothera biennis*). (After Baillon.)

*Narcissi*, *Gladioli*, and *Crocuses* (e.g. *Gentiana Bavaria*, *Narcissus poeticus*, *Gladiolus segetum*, *Crocus sativus*; cf. figs. 279<sup>4, 5, 7</sup>).

The pollen, when deposited, is held between the papillæ of the stigma like dust on velvet pile or on a brush or comb; nor is it absolutely necessary that the stigmatic papillæ should be sticky, though, of course, the power of retention is thus obviously increased. Some stigmas are beset with transparent papillæ, and at the same time are rendered very sticky by a layer of fluid secreted by the surface cells of the stigma, as, for example, in the Sundew (*Drosera*; cf. 279<sup>10</sup> and 279<sup>11</sup>). But such cases are rare on the whole. Usually the velvety stigmas and those beset with long papillæ are not sticky, the viscosity being restricted to wart-like and granulated stigmas. Examples of plants with very sticky

stigmas are furnished by the Umbelliferae, the Rhododendrons, Bearberries, Ericas, Whortleberries and Cranberries, Winter Greens and Polygonums, the Deadly Nightshade, and Bartsias. A sticky stigma often terminates a thin threadlike style either as a small disc or head, and is the more conspicuous on account of the glitter of its sticky coating than because of its size. In the flower of the Mahogany-tree (*Swietenia Mahagoni*; see fig. 282<sup>3</sup>) it has the form of a disc, in *Azalea procumbens* (see fig. 279<sup>17</sup>) it is slightly convex with five projecting ridges radiating from the

centre, in the Prickly Pear (*Opuntia*; see fig. 279<sup>15</sup>) it forms a sinuous fleshy swelling which winds about the end of the style, whilst in the Evening Primrose (*Oenothera*; fig. 281) it is composed of four fleshy lobes arranged in a cross. It is noticeable that sticky stigmas occur most frequently in plants whose pollen is liberated from the sprinkler-like anthers as flour or dust. Such flowers also, the pollen of which consists of quartets (tetrads) of cells surrounded and entangled in delicate threads, are characterized by very sticky stigmas (*cf.* fig. 219<sup>2</sup>, p. 101). In most of the plants mentioned above the pollen adheres so firmly to the stigma at the moment of contact that it cannot be removed even by blowing or vigorous shaking. Many of the sticky stigmas remind one of limed twigs, especially as the sticky layer which produces the adhesiveness is exposed to the air and yet does not dry up, but remains sticky and viscous like bird-lime for several days.

In many instances the stigma does not become sticky until the stigmatic tissue is capable of inciting the pollen-cells which come in contact with it to put out pollen-tubes. The stigma of *Cephalaria alpina*, one of the Dipsacæ, is very remarkable in this respect. Shortly after the corolla has opened, the stigma appears to be completely matured, and as if capable of retaining pollen. But this is not really so. Any pollen placed on it immediately slides off its smooth surface. Not until two days later when the stigmatic tissue has become covered with a delicate layer of sticky fluid, scarcely visible to the eye, is the pollen held fast, and at once puts out pollen-tubes which penetrate into the tissue. But, as in so many other cases, it is impossible to generalize on this point, thus in most Umbelliferae the stigmas are sticky before their tissue is able to influence the pollen in this way. Also, in the flowers of *Allium Victorialis*, the pollen adheres to the stigmas before these are capable of inciting the emission of pollen-tubes, indeed, at the time of attachment the stigmatic papillæ are not even developed. The stigmas of Orchids are sticky some time before the ovules are matured. In these cases the sticky layer has to retain the pollen until the changes have been completed in the deeper stigmatic tissue which will stimulate the pollen to put out its tubes.

It is necessary to give a special description of the manner in which the pollen is deposited on these sticky Orchid stigmas. The stigma of the Helleborine (*Epipactis latifolia*), illustrated in fig. 268, p. 255, has the form of a rectangular table, and is placed opposite the boat-like labellum, which is filled with honey. When a wasp, in licking out the honey, strikes its head against the projecting rostellum at the upper margin of the stigma it adheres for a moment. The two club-shaped masses of pollen which are connected with the rostellum are thus torn out of the loculi of the anthers, and removed by the wasp as it flies away. The wasp now carries the pair of pollen-masses on its head as shown in fig. 268<sup>6</sup>. At first these pollinia stand erect, but after a few minutes they alter their position. In consequence of drying, the masses, composed of adhering groups of pollen-cells, twist and become deflected, and now appear as two thick cushions lying on the front of the head (see fig. 268<sup>7</sup>). This bending is absolutely necessary if the pollen is to be brought by the wasp to the sticky stigma of another flower. If the wasp came with erect pollen-masses to

lick up the honey they would be knocked off by the rostellum, and their aim would either fail entirely or be but partially achieved. But, as soon as the little clubs have bent down over the front of the wasp's head, they are planted by this honey-licking insect exactly on the sticky rectangular stigmatic surface. Each quartet of pollen-cells forms a round or irregularly rectangular ball, and these, connected together by viscous threads, are again grouped so as to form the club-like pollen-mass. When this club is placed on the sticky stigma, all the pollen-quartets which come into contact remain attached, so that when the insect flies away it is much more likely that the sticky threads in the interior of the pollen-mass will be torn than that the pollen adhering to the stigma will be removed again. These two contrivances, so important for the deposition of the pollen on the stigma, viz. the twisting and bending of the originally erect pollen-masses and the tearing of the fine threads which connect the quartets of pollen-cells, occur not only in the Helleborine (*Epipactis*), which has been chosen as an example, but also in many other Orchids which adorn our woods and meadows—especially in the genera *Orchis*, *Gymnadenia*, and *Habenaria*. In the *Epipogium* (see fig. 257, p. 226) the floral contrivances are rather different. Each pollen-mass is chained on one side by the thick strand which leads to the sticky rostellum (fig. 257<sup>11</sup>). When these masses are torn from their hiding-place by a humble-bee (257<sup>13</sup>) they bend round, and now hang on their supports like two cherries on their stalks. In this way the structure, torn from the anther, becomes somewhat elongated—an important change—since it renders it possible that the clubs should reach the stigma in the next *Epipogium* flower visited. In this plant the stigma stands above the rostellum, and the pollinia can only be pressed by flying humble-bees against the stigma if they have long stalks.

Each of these contrivances shows afresh how exact must be the correlation of all the organs which participate in the transference of pollen, and how well they must be regulated if the success of the flower is to be ensured. The alteration of a millimetre in the position of the stigma will prevent the pollen being deposited on the right place and the consequent fertilization. In many cases a still slighter alteration would be hurtful. In some plants only a very limited area of the stigma is able to incite the pollen to emit pollen-tubes. In Asters, as will be shown more in detail presently, it is only a narrow border at the edge of the minute stylar branch, and in many Labiatae it is only the tip of the lower branch of the stigma on which pollen can be deposited with successful results. *Sarracenia purpurea* possesses one of the largest stigmas. It has the form of a sunshade of 3.5 cm. diameter, with five indented lobes round the edge, and the margin of each lobe is furnished with a small tooth on the inside (see fig. 279<sup>6</sup>). These teeth alone are fitted to receive pollen, and if the term stigma is to be restricted to the tissue on which the pollen can eventually develop and put out pollen-tubes, it will only refer in *Sarracenia* to these five tiny teeth. The same is true of *Physostigma venenosum* (see figs. 282<sup>1</sup> and 282<sup>2</sup>) whose bladder-like stylar termination, described as the stigma, is only capable of real pollination over a small part beset with papillæ. It should also be noted here that the papillæ which are developed on the outer side of the stylar



branches in Compositæ, and which at first sight might be mistaken for stigmatic papillæ, do not deserve this appellation. Their function is only to sweep the pollen out of the anther-tube, and their significance will be repeatedly spoken of later in the chapter devoted to autogamy.

The deposition of pollen on the stigma is followed not only by alterations in the pollen-cells and in the stigmatic tissue, but also in other parts of the flower, especially the corolla. The visible changes in the stigma are the withering, shrivelling, and turning brown of its superficial cells. In those plants described above, on



Fig. 232.—<sup>1</sup> *Physostigma venenosum*. <sup>2</sup> Pistil of this plant, removed from the flower; magnified. <sup>3</sup> Flower of *Swietenia Mahagoni*. (After Baillon.)

whose sticky stigmas the pollen is not immediately stimulated to send out pollen-tubes, weeks sometimes elapse before these alterations occur; in others, however, they are to be observed in a few hours. Solanaceous plants are very noticeable in this respect, especially *Nicandra physaloides*, and the Deadly Nightshade (*Atropa Belladonna*). An hour after pollen is deposited on the sticky stigma, it begins to wither and turn brown, and the whole style alters and drops off the ovary. Here, then, the pollen-tubes must have been emitted as soon as the pollen-cells came in contact with the stigmatic tissue, and they reach the ovules in the interior of the ovary within a few hours.

The changes which occur in the petals are even more noticeable. As soon

as the stigma is withered they begin to wither also, or they become detached from the flower and fall off. The withering of the petals occurs in very many ways. They lose their turgidity, shrink up, occupy less space, and at the same time change their colour. A change takes place in the petals of most flowers which last only a day, a change similar to that which occurs in foliage-leaves which have passed through a sharp night frost in autumn and then been exposed next day to the sun—*i.e.* they exude water from their tissue and become pulpy and look as if they had been squashed or boiled. The corollas of some Papilionaceæ, especially several species of the Clover genus (*Trifolium*), dry up and rapidly become like withered leaves. The mean between these two instances is furnished by those numerous plants whose flowers become limp, shrink up somewhat, bend over, and then when withered fall off, as, for example, in most Cruciferae, Valerians, and Compositæ. The petals in withering often assume the position which they occupied originally in the bud. Thus, for example, the tongue-shaped flowers of the Goat's Beard (*Tragopogon*) roll together into a tube on withering, and thus have the same appearance as just before blossoming. Of course this is not always the case, for the tongue-flowers of *Bellidiastrum* and of most Asters roll spirally outwards when they fade, those of *Hieracium staticifolium* spirally inwards, and it is not rare for fading, drying, and discolouring petals to undergo corkscrew-like torsions. The connection between the withering and the discoloration which accompanies it has already been mentioned (p. 222). In many plants it happens that petals drop from the flower either singly or all together after the deposition of pollen on the stigma without having previously withered at all. Examples are furnished by Roses, Almonds, Primulas, and Fuchsias.

It has been repeatedly shown by researches instituted for the solution of the question that the sudden withering and falling of the petals is really dependent on the deposition of pollen on the stigma, *i.e.* on the penetration of pollen-tubes into the stigmatic tissue. If of two flowers which open simultaneously one is provided with pollen and the other is shielded from it, or rather if the stigma of one flower is purposely pollinated while the other is guarded from the deposition of pollen, the latter will last longer and will not fall as soon as the former. In two blossoms of a Flax (*Linum grandiflorum*), which opened at the same time and were treated in this way, the corolla remained 35 hours on the flower whose stigma was pollinated, but 80 hours on the other flower whose stigma had received no pollen. Of two flowers of *Anagallis Philippi* the corolla fell in four days from the one which had been pollinated, but remained for six days on the flower whose stigma had been protected from pollen. In a plant of *Mammillaria glochidiata* the flowers which were pollinated appeared pulpy and permanently closed two days before those whose stigmas remained free from pollen. Orchids as cultivated in hot-houses offer a very well-marked example of this same property. Normally these flowers are free from insect-visits in the hot-house and their flowers remain fresh for many

days, and in some instances for weeks. If, however, the stigmas of these same plants be artificially pollinated, a quick collapse of their showy perianths is observed. If the view that the gaily-coloured corollas act primarily as allurements to insects which visit flowers and transfer pollen require strengthening these results are certainly found to be in accordance. As soon as the end is gained, *i.e.* as soon as the stigma is pollinated, the further allurements of insects is unnecessary; the petals therefore immediately cease working, fall off or wither, and are no longer divergent—in a word, they have ceased to act as an allurements to insects. This phenomenon can only be explained by supposing that the changes produced in the tissues of the stigma by the developing pollen-grains take effect in ever-widening circles which at length reach the petals, and that by what we may term the stimuli, transmitted from the stigmatic tissue and the ovary to the corolla, a sudden separation between the petals and the rest of the flower and an equally sudden alteration in the turgidity of the petals are brought about.

It only remains to be mentioned that the early withering and fall of the petals of those flowers which are pollinated soon after opening has a counterpart in the phenomenon of the long duration of double flowers. Double flowers, in particular those whose stamens and carpels have been transformed into petals, remain fresh two, three, even eight days longer than the normal single flowers of the same kind, as may be seen, for example, in Pelargoniums, Tulips, Pinks and Stocks.

#### THE CROSSING OF FLOWERS.

While Goethe was staying at Carlsbad a young gardener every day brought him a bunch of flowering plants from the visitors assembled at the waters and undergoing the cure. Both men and women were greatly interested in ascertaining the names of these plants with the assistance of the writings of the Swedish botanist Linnæus, whose fame had at that time spread far and wide. This searching for names was called the “naming” or “determining” of plants, and it was prosecuted with great zeal by dilettanti as a sort of puzzle-game and as a pleasant, stimulating pastime. Even in professional circles Linnæus found a recognition which has rarely been accorded to a contemporary. His method had taken the whole world by storm, and his “system” was everywhere in the ascendant. Of course individual voices were raised against the new teaching, chiefly indeed from the dilettanti. Goethe relates that many of the Carlsbad visitors designated the pursuit of the knowledge of the Vegetable Kingdom according to the Swedish botanist as senseless play which satisfied neither the understanding nor the imaginative faculty, and could relieve no one of ennui. Evidently Goethe also had perceived the weakness of the Linnean method. Besides, he was not concerned with counting or numbers nor the distinction of forms founded on insignificant points; he was not interested in the differences of plants, but rather in what they had in common and in what bound the



Vegetable Kingdom into a many-membered whole. It is therefore obvious that he could never have felt much enthusiasm for the Swedish botanist.

But, strange as it may sound, that which Goethe regarded as the weak point in the Linnean system was, on the contrary, its strength. The very fact that counting afforded a safe path through the apparent chaos of plant-forms, that by means of counting the floral parts the possibility was afforded of attaining to a short and intelligible classification; and not least, the persistent adherence to the principles laid down fascinated both lay and professional men. These same good points explain why even many quite recently issued works (tourists' pocket-floras and the like) retain the Linnean system when their object is to facilitate a speedy reference of a plant to its position amid the plexus-like ramifications of the phylogenetic tree. Later on we shall have an opportunity of investigating the value of the different plant-systems from an historical standpoint. Here the Linnean system claims our attention solely on the ground of the division of the stamens and pistil, *i.e.* of those organs in which the two kinds of sexual cells are formed. The results of the researches into the divisions of these organs in which the fertilizing and receptive sexual cells, *i.e.* the male and female cells are developed, form the foundation of the Linnean system and afford the most important marks for the division into the so-called Classes, of which Linnæus distinguished twenty-four.

The first 20 classes of the Linnean system include Phanerogams, whose flowers are all hermaphrodite, *i.e.* in which each flower of the plant contains both stamens and pistil. Those species whose stamens are all the same length, and are neither joined to one another nor to the pistil, are all in the first 13 classes. Each of these 13 classes is distinguished in the following manner:—

CLASS.

1. MONANDRIA. A single stamen in each flower; *e.g.* Mare's-tail (*Hippuris*), Indian Shot (*Canna*), *Alpinia* (see fig. 283<sup>1</sup>).
2. DIANDRIA. Two stamens in each flower; *e.g.* Speedwell (*Veronica*; see fig. 257<sup>1</sup>), Lilac (*Syringa*; see fig. 283<sup>2</sup>).
3. TRIANDRIA. Three stamens in each flower; *e.g.* *Iris* (see fig. 265, p. 246), Valerian (*Valeriana*; see fig. 283<sup>3</sup>).
4. TETRANDRIA. Four stamens in each flower; *e.g.* Woodruff (*Asperula*), Plantain (*Plantago*), Cornel (*Cornus*; see fig. 283<sup>4</sup>).
5. PENTANDRIA. Five stamens in each flower; *e.g.* Deadly Nightshade (*Atropa*), Cowbane (*Cicuta*), *Aralia*; (see fig. 283<sup>5</sup>).
6. HEXANDRIA. Six stamens in each flower; *e.g.* Tulip (*Tulipa*), Lily of the Valley (*Convallaria*), *Gagea* (see fig. 283<sup>6</sup>).
7. HEPTANDRIA. Seven stamens in each flower; *e.g.* Horse Chestnut (*Æsculus Hippocastanum*; see fig. 283<sup>7</sup>).
8. OCTANDRIA. Eight stamens in each flower; *e.g.* Ling (*Calluna*), Spurge Laurel (*Daphne*; see fig. 283<sup>8</sup>).
9. ENNEANDRIA. Nine stamens in each flower; *e.g.* Bay Laurel (*Laurus*), Flowering Rush (*Butomus*; see fig. 283<sup>9</sup>).

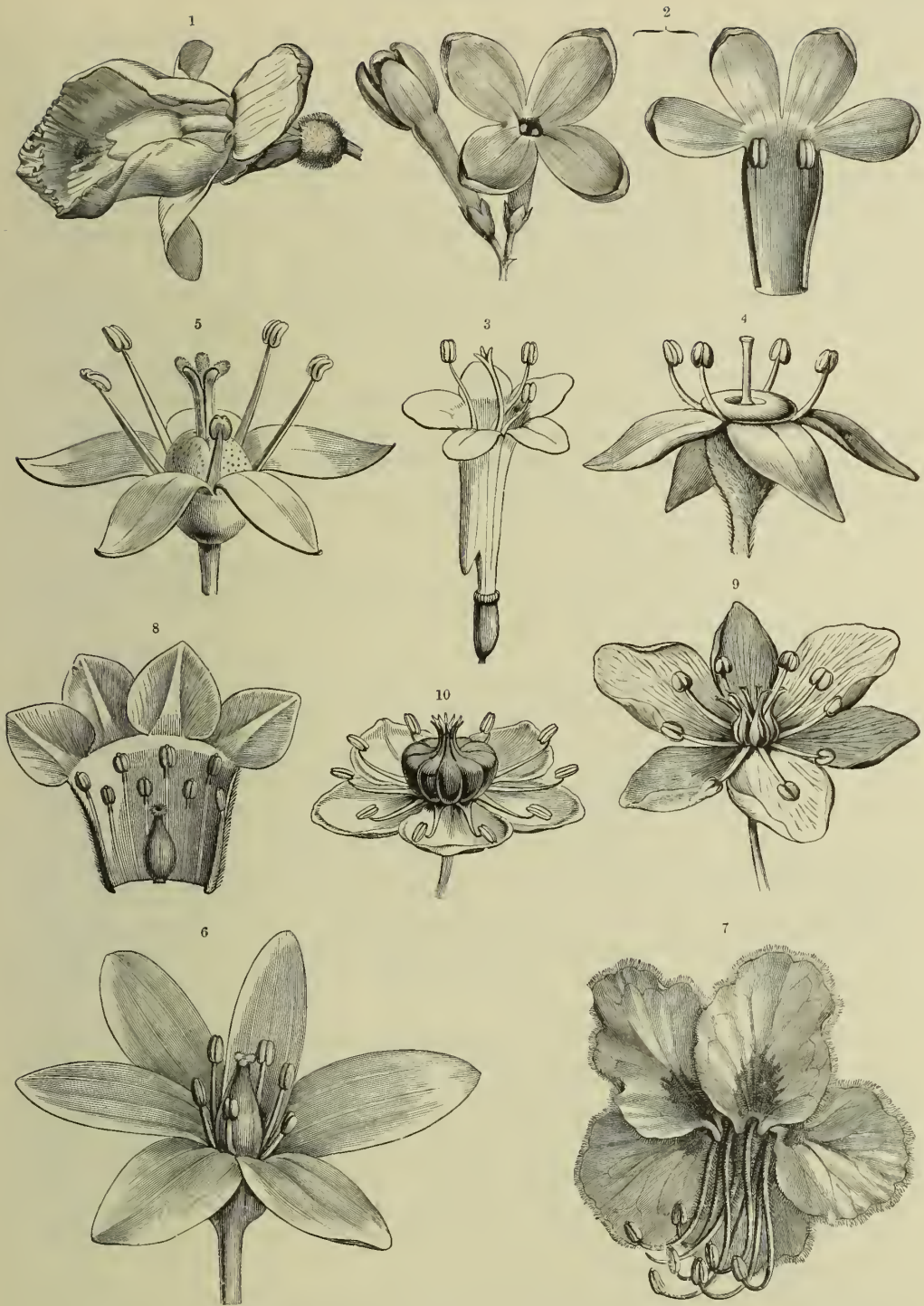


Fig. 283.—Types of the 1st to 10th classes of the Linnean System.

1 *Alpinia*. 2 *Syringa vulgaris*. 3 *Valeriana officinalis*. 4 *Cornus mas*. 5 *Aralia Japonica*. 6 *Gagea lutea*. 7 *Æsculus Hippocastanum*. 8 *Daphne Mezereum*. 9 *Butomus umbellatus*. 10 *Phytolacca decandra*. All the flowers somewhat enlarged.

VOL. II.

## CLASS.

10. DECANDRIA. Ten stamens in each flower; *e.g.* Rue (*Ruta*; see fig. 290), *Phytolacca* (see fig. 283<sup>10</sup>).
11. DODECANDRIA. Number of stamens not quite definite, 11–20 in each flower; *e.g.* Mignonette (*Reseda*), House-leek (*Sempervivum*), Agrimony (*Agrimonia Eupatoria*; see figs. 285<sup>1</sup> and 285<sup>2</sup>).
12. ICOSANDRIA. More than twenty stamens in each flower, situated on the edge of the cup-shaped receptacle (or calyx-tube), their position, therefore, being *above* or *on a level* with the stigma; *e.g.* Rose (*Rosa*), Almond (*Amygdalus*), *Calycanthus*; see fig. 285<sup>3</sup>) *Chrysobalanus* (see fig. 285<sup>4</sup>).
13. POLYANDRIA. 20–200 stamens in each flower, springing from the receptacle *below* the pistil; *e.g.* Poppy (*Papaver*), Lime (*Tilia*; see figs. 284<sup>1</sup> and 284<sup>2</sup>) and *Anemone* (see fig. 284<sup>3</sup>)  
 In the 14th and 15th Classes Linnæus puts all Phanerogams with hermaphrodite flowers in which the stamens are unequal in length.
14. DIDYNAMIA. Includes flowers with four stamens, two long and two short; *e.g.* the Foxglove (*Digitalis*), Snapdragon (*Antirrhinum*; see fig. 284<sup>6</sup>).
15. TETRADYNAMIA. Includes flowers with six stamens, four long and two short; *e.g.* Mustard (*Sinapis*), Wall-flower (*Cheiranthus*), Bitter-cress (*Cardamine*; see figs. 284<sup>7</sup> and 284<sup>8</sup>).  
 The 16th–20th Classes include all Phanerogams whose stamens are joined in any way either to one another or to the pistil. They are distinguished from one another thus:—
16. MONADELPHIA. The filaments of all the stamens of a flower are joined into a tube; *e.g.* Tamarind (*Tamarindus Indica*; see fig. 284<sup>9</sup>), Hollyhock (*Althæa*), Mallow (*Malva*), Baobab (*Adansonia*; see fig. 284<sup>10</sup>).
17. DIADELPHIA. The filaments of the stamens are united and form two groups; *e.g.* Milkwort (*Polygala*), Fumitory (*Fumaria*; see figs. 285<sup>5</sup> and 285<sup>6</sup>).
18. POLYADELPHIA. The filaments of the stamens are united and form three or more groups; *e.g.* St. John's Wort (*Hypericum*), *Melaleuca*; (see figs. 284<sup>4</sup> and 284<sup>5</sup>).
19. SYNGENESIA. The anthers of the stamens in each flower are joined together into a tube; *e.g.* in *Lobelia*, Hawkweed (*Hieracium*; see figs. 222<sup>4</sup> and 222<sup>7</sup>, p. 112).
20. GYNANDRIA. The stamens are united with the pistil; *e.g.* the Orchids: *Phalænopsis*, (see figs. 258<sup>1</sup> and 258<sup>2</sup>, p. 227); *Cypripedium* (see figs. 267<sup>1</sup> and 267<sup>2</sup>, p. 249); *Epipactis*; see figs. 268<sup>2</sup> and 268<sup>3</sup>, p. 255); also the Birthwort (*Aristolochia*; see figs. 284<sup>11</sup> and 284<sup>12</sup>).  
 Now come those plants whose flowers are not hermaphrodite or not all hermaphrodite, and these are distinguished in the following way:—
21. MONŒCIA. Flowers monœcious, *i.e.* the flowers which contain only stamens or only pistils, are separated but grow on the same plant, *e.g.* the Maize (*Zea Mais*), the Oak (*Quercus*; see fig. 286); the Castor-oil Plant (*Ricinus*; see figs. 285<sup>7</sup> and 285<sup>8</sup>), *Croton* (see figs. 285<sup>11</sup> and 285<sup>12</sup>), *Liquidambar* (see figs. 285<sup>9</sup> and 285<sup>10</sup>).
22. DIOECIA. Flowers dioecious, *i.e.* the flowers containing stamens only are found on certain plants, and those with pistils only on other plants; *e.g.* the Willow (*Salix*; see fig. 287).
23. POLYGAMIA. Flowers polygamous, *i.e.* staminate, pistillate, and hermaphrodite flowers are all found either on the same or on different plants, in various ways; *e.g.* the Ash (*Fraxinus*; see fig. 230, p. 138).
24. CRYPTOGAMIA. Includes Non-flowering Plants.



Linnæus described 20 out of the 23 Classes of Phanerogams as hermaphrodite. He considered hermaphrodite flowers generally to be the rule, and thought them more complete than the unisexual. He connected their prevalence directly with the formation of fruit, and believed the presence of stamens and pistils in the same flower could be explained most simply and naturally by the fact that fertilization could be performed much more easily when the receptive and fertilizing organs were in immediate proximity than when they were widely separated, and thus the formation of seeds capable of germination be best ensured. In a word, the idea originated and found expression afterwards as an actual doctrine that fertilization begins in hermaphrodite flowers by the transference of the pollen on to the stigma of the same flower, *i.e.* that the process occurs which we now call *autogamy* or self-fertilization. More recent researches, however, have shown that many plants are only apparently (or pseudo-) hermaphrodite; that stamens and carpels indeed stand close together in their flowers, but that the pollen-grains in the anthers are not properly developed and have lost their fertilizing capacity. In other flowers, regarded as hermaphrodite, the ovules are so altered that they are unable to develop into seeds capable of germination. It has also been shown that plants provided with both unisexual and hermaphrodite flowers, which Linnæus called polygamous and placed in the 23rd Class, occur much more frequently and in much greater variety than was formerly supposed. There is a long series of forms, one limit of which is constituted by plants with truly hermaphrodite flowers, and the other by diœcious plants. It is impossible, for want of space, to give an exhaustive description of all the members of this series; but since it is important, for the sake of what follows, to obtain as clear an idea as possible of this matter, the chief members of the series at any rate will now be enumerated.

At one end of the series, then, are the bisexual flowers. They always contain one or several stamens besides the ovary. In the ovary are developed the ovules which after successful fertilization become seeds capable of germinating; whilst the anthers of the stamens contain pollen grains which have the power of fertilizing. These flowers are termed *hermaphrodite* and it is desirable to emphasize the expression by speaking of them as truly hermaphrodite flowers.

The unisexual flowers come next. In these only one of the two sets of organs which take part in fertilization is fully matured and able to perform its function. When only the pistil is present, with ovules capable of development, and the stamens do not mature or are entirely absent, the flowers are called female or pistillate; flowers which contain stamens only, with fertile pollen, whose pistil does not mature or is altogether absent, are termed male or staminate. Four kinds of unisexual flowers may be distinguished: (1) Pistillate flowers which appear hermaphrodite. In these pistil and stamens are present, and these flowers therefore seem at first sight to be bisexual. Their pistil contains ovules which can be fertilized and are capable of development, but the cells which are formed in the tissues of the anthers have no fertilizing power. (2) Staminate flowers which appear hermaphrodite. These are the counterpart of the first group. They also contain both



Fig 284.—Types of the 13th, 14th, 15th, 16th, 18th, and 20th classes of the Linnean System.

- 1, 2 *Tulia*, whole flower and section of same. 3 *Anemone nemorosa*. 4, 5 *Melaleuca*, whole flower and section of same.  
 6 *Antirrhinum*, upper lip of corolla showing stamens. 7 *Cardamine pratensis*. 8 The same flower, the petals removed.  
 9 *Tamarindus*. 10 *Adansonia*. 11 *Aristolochia Clematitis*. 12 The same flower after removal of the perianth.  
 6, 9, 10, 11 natural size; the others somewhat magnified.





Fig. 235.—Types of the 11th, 12th, 17th, and 21st classes of the Linnean System.

<sup>1, 2</sup> *Agrimonia Eupatoria*, whole flower and section of same. <sup>3</sup> *Calycanthus*, cut through longitudinally. <sup>4</sup> *Chrysobalanus*, longitudinal section of flower. <sup>5</sup> *Fumaria officinalis*, whole flower. <sup>6</sup> The same flower after the removal of the petals. <sup>7</sup> Staminate flower of *Ricinus communis*. <sup>8</sup> Pistillate flower of *Ricinus communis*. <sup>9</sup> Staminate flower of *Liquidambar*. <sup>10</sup> Pistillate flower of *Liquidambar*. <sup>11</sup> Staminate flower of *Croton*. <sup>12</sup> Pistillate flower of *Croton*, both halved. All the figures somewhat enlarged.



stamens and pistil, and so might also be mistaken for hermaphrodite flowers, but closer examination shows that their ovaries do not develop sufficiently to produce fertile seeds. The ovules, and usually the stigmas as well, do not mature, but the pollen in the anthers attains its full power. (3) True pistillate flowers. In these only fertile ovaries are developed, and there is no trace of stamens. (4) True staminate flowers, the counterpart of the third group. They contain stamens whose anthers hold ripe pollen, but their ovaries are quite suppressed.

To the four types of unisexual flowers we shall apply short descriptive names, at once rendering the character of the flower apparent, and saving much needless iteration and confusion. (1) *Pseudo-hermaphrodite female flowers* are the pistillate flowers which appear to be hermaphrodite, similarly (2) *Pseudo-hermaphrodite male flowers* are the staminal flowers which, from the presence of reduced pistils, appear to be hermaphrodite. (3) True *pistillate flowers*, and (4) True *staminate flowers*.

Next to the unisexual come the neuter (sterile) flowers, in which the ovaries and stamens are either altogether absent, the flower consisting merely of petals and sepals, or the sexual organs if present are quite rudimentary and hidden away in the centre of the flower.

The kinds of flower enumerated here are connected together by numerous transitional forms. In the hermaphrodite flowers of the Knawel (*Scleranthus*) two or three of the four stamens are often sterile; they occupy their right position, but their anthers are shrivelled and contain no ripe pollen, only one or two of the stamens being properly developed. Of the eight stamens of the well-known garden-plant *Clarkea pulchella* only the four which alternate with the petals form fertile pollen, while the anthers of the other four are abortive. Sometimes five, six, seven, or even all the anthers are sterile. The Chickweed (*Stellaria media*) has ten stamens arranged in two whorls of five, but it rarely happens that all the anthers produce fertile pollen. Usually those of the five inner and often of a pair of the outer whorl are shrivelled and have no pollen. These instances evidently form good links between the true hermaphrodite and the pseudo-hermaphrodite flowers. The flower-heads of the Burnet (*Poterium polygamum*) consist of pistillate, staminate, and truly hermaphrodite flowers. In the staminate flowers sixteen stamens are formed; the hermaphrodite flowers may contain eight, seven, six, or gradually decreasing numbers down to only one. The other stamens are not even formed, not the slightest trace of them can be found. These flowers may be regarded as connecting the truly hermaphrodite with the pistillate flowers, for if the suppression of stamens be supposed to go still further, so that the last stamen has disappeared, then the flower is no longer hermaphrodite, but has become a true pistillate flower.

The gradations in the class of pseudo-hermaphrodite, pistillate, and staminate flowers are also very varied. The Fuller's Thistle (*Cirsium*), the Flowering Ash (*Fraxinus Ornus*), the Asparagus (*Asparagus officinalis*), the Date-plum (*Diospyros Lotus*), the Vine (*Vitis vinifera*), many Scabiouses, Saxifrages, Valerians, &c., all

develop imperfect flowers, which are liable to be mistaken at first sight for truly hermaphrodite. They have plain well-developed ovaries, and stamens in whose anthers pollen-grains are formed in greater or less numbers; but experiments with this pollen have shown that when deposited on the stigma it emits no pollen-tubes, and consequently the flowers are not in reality truly hermaphrodite, but only apparently so. This is the case in some of the flowers in the panicle of the Horse Chestnuts (*Æsculus* and *Pavia*), in some species of Dock (*Rumex alpinus*, *obtusifolius*, &c.), and in some of the flowers in the centre of the heads of the Colt's-foot, Marigold, and Butter-bur (*Tussilago*, *Calendula*, *Petasites*). They appear hermaphrodite although the ovaries never form fruits with fertile seeds, because their stigmas are not capable of inciting the emission of pollen-tubes in the ripe pollen deposited on them. Again, there are many plants where either the ovaries or the stamens are so reduced that they can only be discovered by careful searching. Some examples of the red Campion (*Lychnis diurna*) have flowers with well-developed ovaries and stigmas, which are capable of fertilization, while their stamens are extremely minute, consisting of triangular bodies scarcely 1 mm. long, which bear a small polished head destitute of pollen instead of an anther. Other plants of this same Campion bear flowers with ten stamens whose long ribbon-like filaments are surmounted by large anthers with fertile pollen, but instead of the ovary there is only a minute knob with two points indicating the stigma. The same thing occurs in the flowers of some Valerians (*Valeriana dioica*, *simplicifolia*, &c.). The racemes of the Sycamore (*Acer Pseudo-platanus*) exhibit every imaginable gradation from pseudo-hermaphrodite male flowers, with comparatively large ovaries, to those in which the ovaries are reduced or altogether absent. I have mentioned these instances, to which many others might be added, to show that there is no lack of transitional forms between pseudo-hermaphrodite and truly pistillate and staminate flowers; and again, in plants with neuter flowers, especially in many species of the Grape-Hyacinth (*Muscari*), we have gradations from truly-hermaphrodite to neuter flowers. The remarkable structures known as gall-flowers (*cf.* pp. 159, 160) may also be mentioned here. They represent neuter flowers, and occasionally undoubted links are found between them and true pistillate flowers. In spite of these transitional forms, which to some extent break down the limits between the various kinds of flower, it is advisable to retain the names already used for the separate forms, since otherwise it would be impossible to give a general account of the arrangement of the sexes in Phanerogams.

It has been stated above that botanists were formerly content with dividing plants according to their sex into those with hermaphrodite, monœcious, diœcious, and polygamous flowers (*cf.* p. 291). This classification, however, is no longer adequate to the present standpoint of our knowledge. I will now attempt to give an approximate account of the extremely complex conditions which must be considered in this matter, but will keep to the old divisions as far as possible in so doing.

We may place in the first group those plants whose species develop true herma-

phrodite flowers exclusively. Although this group is not so comprehensive as it was thought to be in the time of Linnæus, it is nevertheless the most important, and includes more than a third of all the Phanerogams. The *Alpinia*, Lilac, Cornel, *Gagea*, Spurge Laurel, Flowering Rush, *Phytolacca*, Agrimony, Lime, Anemone, Bitter-cress, Baobab, and *Melaleuca*, all figured on pp. 289, 292, 293, may be mentioned as examples.

Close to these comes a second group of species which bear pseudo-hermaphrodite female flowers as well as truly hermaphrodite flowers, as, for example, *Oxyria digyna* and *Geranium lucidum*.

The third group includes those species whose individuals develop both true hermaphrodite flowers and those which appear to be so, but are really pseudo-hermaphrodite male flowers. Though instances of the second group are rare, the third comprises hundreds of species from widely-different families. Special instances are furnished by the North American Shrubby Trefoil (*Ptelea trifoliata*), the common Bistort (*Polygonum Bistorta*), the Horse-Chestnuts (*Æsculus*, *Pavia*), some Aralias (e.g. *Aralia nudicaulis*), several species of Bed-straw and Woodruff (e.g. *Galium Cruciata*, *Asperula taurina*), and many Umbelliferæ. In the last-named the arrangement and distribution of the two kinds of flowers is quite determinate for each genus, and has the closest connection with the processes of pollen-transfer. In *Anthriscus* the umbellate heads of the central umbel contain for the most part true hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers. The heads of the lateral umbels, however, are composed entirely of these staminate flowers. In *Caucalis* the central umbellate heads consist exclusively of pseudo-hermaphrodite male flowers, while the other heads are formed of 2 true hermaphrodite flowers and 4-7 pseudo-hermaphrodite male flowers. In *Astrantia* the large central umbels contain 12 hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers, but the lateral, smaller umbels contain the latter only. *Athamanta cretensis*, *Chærophyllum aromaticum* and *Meum Mutellina* have in all their umbels a central hermaphrodite flower surrounded by staminate flowers (i.e. male pseudo-hermaphrodites), and these in turn are surrounded by true hermaphrodite flowers. All the umbels of *Chærophyllum Cicutaria* and *Laserpitium latifolium* contain short-stalked pseudo-hermaphrodite male flowers surrounded by long-stalked truly hermaphrodite flowers. In the centre of all the umbels of *Turgenia latifolia* are 6-9 pseudo-hermaphrodite flowers which do not radiate, and 5-8 true hermaphrodite flowers, ray-like on the circumference; whilst in *Sanicula europæa* there are three central hermaphrodite flowers in each umbel surrounded by 8-10 pseudo-hermaphrodite male flowers.

In the fourth group each plant bears both truly hermaphrodite and truly pistillate flowers. A large number of Composites come under this heading, of which the Asters may be taken as a type (*Aster*, *Bellidiastrum*, *Stenactis*, *Solidago*, *Bupthalmum*, *Inula*, *Arnica*, *Doronicum*, &c.). The tubular florets of the disc are truly hermaphrodite in each capitulum, while the tongue-shaped ray-florets are truly pistillate. This division of the sexes also occurs in other Compositæ, of which



the genera *Homogyne* and *Helichrysum* may be taken as typical, where the ray-florets are not tongue-shaped but threadlike. This arrangement is rarely met with except in these Composites. Strangely enough, it occurs in a species of *Gladiolus* (*Gladiolus segetum*).

The fifth group is made up of species where every plant bears both hermaphrodite and true staminate flowers. For examples we have the so-called White Hellebore (*Veratrum*), the Crown Imperial (*Fritillaria imperialis*), the Snake-root (*Calla palustris*), and numerous Grasses belonging to the genera *Andropogon*, *Arrhenatherum*, *Hierochloa*, *Holcus*, and *Pollinia*.

A sixth group comprises those species in which every plant bears both true pistillate and pseudo-hermaphrodite male flowers, but none that are truly hermaphrodite. In this group are placed the Marigold (*Calendula*), the Colt's-foot (*Tussilago*), and *Micropus*. Here tubular staminate flowers (which are really pseudo-hermaphrodite) occupy the centre of the capitulum, and true pistillate flowers, either tongue-shaped or filiform, occur at the circumference. The Edelweiss (*Gnaphalium Leontopodium*) and the Butter-bur (*Petasites*) also belong to this group. In the two last-named plants, however, the arrangement in the single capitula is of a peculiar kind differing from that in the other Composites mentioned. There are three kinds of individuals of Edelweiss. In one the central head of the whole inflorescence contains only pseudo-hermaphrodite male flowers, whilst in the second form the central capitulum is again formed entirely of pseudo-hermaphrodite male flowers, but in the other capitula these are surrounded by true pistillate flowers. In the third form all the capitula have pseudo-hermaphrodite male flowers surrounded by true pistillate flowers. In the Butter-bur (*Petasites*) all the capitula have pseudo-hermaphrodite male flowers in the centre, and true pistillate flowers around the circumference, but strangely enough the number of these varies from plant to plant. In some plants the pseudo-hermaphrodite male flowers are very numerous, and the capitula contain but few true pistillate flowers and *vice versa*. These two kinds of plants differ very much in appearance, and the Butter-bur might therefore be easily mistaken for a dioecious plant.

The seventh group includes all those species in which each plant develops both true staminate and true pistillate flowers, species which have been previously termed monœcious. Examples of this large group are: Oak (*Quercus*; see fig. 286), Hazel (*Corylus*; see fig. 235, p. 147), Alder (*Alnus*; see fig. 228, p. 135), Walnut (*Juglans*; see fig. 184, vol. i. p. 742), Pine (*Pinus*; see fig. 233, p. 144), many Urticaceæ (*Urtica urens*, *Pachysandra*), numerous Aroids (*Arum*, *Ariopsis*, *Arisema*, *Richardia*, &c.), many Palms, a number of marsh and water plants (*Myriophyllum*, *Sagittaria*, *Sparganium*, *Typha*, *Zannichellia*), some Grasses (*Heteropogon*, *Zea Mays*), and, especially, many Euphorbiaceæ and Cucurbitaceæ.

Species belonging to the eighth group have three kinds of flower side by side on the same plant, *i.e.* pseudo-hermaphrodite male and pseudo-hermaphrodite female flowers and true hermaphrodite flowers. Examples are furnished by various Acers (*Acer Pseudo-platanus* and *platanoides*), Sumachs (e.g. *Rhus Cotinus* and *Toxi-*

codendron), Laurels (e.g. *Laurus nobilis* and *Sassafras*), many Docks (e.g. *Rumex alpinus* and *obtusifolius*), the Wall Pellitory (*Parietaria*), and also some Saxifrages (e.g. *Saxifraga controversa* and *tridactylites*).

The ninth group consists of species whose individuals each bear true hermaphrodite flowers along with true pistillate and true staminate flowers. The Ash

(*Fraxinus excelsior*; see fig. 230, p. 138) is an example of this group.

Now come the groups whose species contain two or three kinds of flowers distributed on two or several plants.

Species belonging to the tenth group bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another. Examples of this are: numerous Valerians (e.g. *Valeriana montana*, *Salicunca*, *supina*), some Dipsacæ (e.g. *Scabiosa lucida*, *Knautia arvensis*), many Saxifrages (e.g. *Saxifraga aquatica*), the cultivated Vine (*Vitis vinifera*), many Caryophyllacæ (e.g. *Dianthus glacialis* and *prolifer*, *Lychnis*



Fig. 236.—Type of a monœcious plant.

<sup>1</sup> Oak (*Quercus pedunculata*); pistillate flowers on the upper part of the twig, staminate flowers (in pendent catkins) below. <sup>2</sup> A single pistillate flower of the same plant.

<sup>3</sup> Three staminate flowers of the same plant. <sup>1</sup> nat. size; <sup>2</sup> and <sup>3</sup>  $\times 4$ .

*Viscaria*, *Silene noctiflora*), and, especially, very many Labiatæ (e.g. *Calamintha*, *Glechoma*, *Marrubium*, *Mentha*, *Origanum*, *Prunella*, *Thymus*).

In the eleventh group we place those plants which develop true hermaphrodite flowers on one plant and pseudo-hermaphrodite male flowers on another, as, for example, numerous Ranunculacæ (e.g. *Ranunculus baldensis*, *Pulsatilla alpina*, *vernalis*, *Ranunculus alpestris*, *glacialis*), many Rosacæ (e.g. *Dryas octopetala*, *Geum montanum* and *reptans*), and many species of Vine (e.g. *Vitis sylvestris*, *macrocarpha*).



The twelfth group comprises those species which bear pseudo-hermaphrodite female flowers on one plant and pseudo-hermaphrodite male flowers on another. This is observed in species of Buckthorn of the section *Curvispina* (*Rhamnus cathartica*, *saxatilis*, *tinctoria*), in various Caryophyllaceæ (e.g. *Lychnis diurna* and *vespertina*), in Asparagus (*Asparagus officinalis*), the Rose-root (*Rhodiola rosea*), the Mountain Currant (*Ribes alpinum*), and the Fuller's Thistle (*Cirsium*).



Fig. 287.—Type of a dioecious plant: Crack Willow (*Salix fragilis*)

1 Twig with pistillate catkins. 2 Twig with staminate catkins. Natural size.

The Mountain Cudweed (*Gnaphalium dioicum*) and the closely allied species of the same genus, *Gnaphalium alpinum* and *carpaticum*, also belong to this group.

The thirteenth group contains numerous species all bearing true pistillate flowers on one plant and true staminate flowers on another; they were termed *diœcious* by Linnæus. Examples are: *Ephedra*, Cycads, Juniper, Yew, and Ginkgo (*Juniperus*, *Taxus*, *Ginkgo*), numerous Sedges (e.g. *Carex Davalliana*, *dioica*), *Vallisneria* (see fig. 155, vol. i. p. 667), Hemp and Hop (*Cannabis*, *Humulus*), the Paper Mulberry (*Broussonetia papyrifera*; see fig. 229, p. 137), Dog's Mercury



(*Mercurialis*), some Docks (*Rumex Acetosa*, *Acetosella*), Sea Buckthorn (*Hippophae*), Poplar (*Populus*), and the Willows, one of which is figured on last page.

The fourteenth group consists of species which bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another, and pseudo-hermaphrodite male flowers on a third plant. Caryophyllaceous plants afford many examples of this group, viz. *Saponaria ocymoides*, *Silene acaulis*, *nutans*, *Orites* and *Saxifraga*. This arrangement is less often met with in Gentians, as, for example, in *Gentiana ciliata*.

A fifteenth group may be added, in which the species have their three kinds of flowers distributed in four ways on different plants, so that they can be divided into four varieties. *Spiræa Aruncus* is typical of this. It produces true hermaphrodite flowers and pseudo-hermaphrodite male and female flowers. The three kinds of flowers are arranged thus: (1) some plants bear only pseudo-hermaphrodite female flowers, (2) others only pseudo-hermaphrodite male flowers, (3) some bear both hermaphrodite flowers and pseudo-hermaphrodite male flowers, and (4) in addition there are yet other plants whose flowers are all hermaphrodite.

To complete this summary it should be mentioned that some species exhibit deviations from their usual distribution of the sexes, although this is not often the case. For instance, plants of the dioecious Nettle (*Urtica dioica*) sometimes occur with both true pistillate and staminate flowers on the same individual. The same thing is occasionally seen in Willows. Most of the plants of the Wild Basil (*Clinopodium vulgare*) in a given locality bear hermaphrodite flowers, but from a few of the flowers on some plants anthers are either partially or wholly absent. Staminate plants of *Vitis cordata* were grown in the Vienna Botanical Gardens and only developed staminate flowers for many years, but occasionally true hermaphrodite flowers appeared as well. Single staminate flowers have been repeatedly observed on the pistillate plants of the dioecious Dog's Mercury (*Mercurialis annua*), and in *Lychnis diurna* and *vespertina* true staminate flowers and isolated hermaphrodite flowers are sometimes found together. Single hermaphrodite flowers occur here and there in the inflorescences of the Castor-oil plant (*Ricinus communis*) among the true pistillate and staminate flowers, and on many plants of *Saponaria ocymoides* true hermaphrodite and pseudo-hermaphrodite female flowers have been seen together with pseudo-hermaphrodite male flowers.

In the light of these results of recent investigation it is evident that the theory expressed in the Linnean System, viz. that the great majority of Phanerogams bear only hermaphrodite flowers, is not confirmed, and that the view held by Linnæus as to the completeness and importance of this type of flower breaks down with it.

But since it is now established that the separation of the sexes in the Vegetable Kingdom is such a widespread phenomenon, it must offer some advantage, and this advantage can only lie in connection with cross-fertilization. By *cross-fertilization* in Phanerogams we mean here the transference of pollen-cells from one flower to

the stigma of another which contains the female sexual cells in its ovary; and we may distinguish between crossing in plants of the *same* and of *different* species. In the former case the pollen of one flower is deposited on the stigma of another flower belonging to a plant of the *same* species; in the latter case the pollen is deposited on the stigma of a flower which is *not of the same* species. Obviously in the latter process, which is also termed *hybridization*, the two flowers are some distance apart. Of the former process there are two varieties, viz. *Geitonogamy* (from *γείτων*, a neighbour, and *γάμος*, marriage), when the two flowers are immediate neighbours, growing upon the same plant, and *Xenogamy* (from *ξένος*, a stranger, and *γάμος*, marriage), when they are on different plants of the same species.

Although the distribution of the sexes on different plants or in different flowers of the same plant has been indicated as advantageous, even as a condition for the occurrence of cross-fertilization, it must not be supposed that it is the only contrivance for ensuring hybridization, xenogamy, or geitonogamy. It is beyond question that the same result is obtained in true hermaphrodite flowers, *i.e.* that plants whose flowers all contain fertile pollen-grains and ovaries which are capable of development can cross with one another. Of course special arrangements are necessary for this, and the more important of them will be mentioned in the following pages and illustrated by a few examples. In some instances cross-fertilization is unavoidable from the mutual arrangement and position of the two kinds of sexual organs which occur together in a true hermaphrodite flower. If during the whole time of flowering the stigma assumes such a position as to be brushed by an insect which is visiting the flower, but at the same time is so placed that it cannot receive the pollen from the anthers immediately surrounding it, it may be safely assumed that it is adapted to cross-fertilization. This is the case, for example, in the White Lily (*Lilium album*), Day Lily (*Hemerocallis flava* and *fulva*), *Anthericum*, and numerous bulbous plants of the Cape (*Amaryllis*, *Albuca*, &c.) The entrance to these flowers is directed laterally, and the style projects so far beyond the anthers with their sticky pollen that its stigma never receives any of it. On the other hand, when the projecting style is used as a resting-place by flying animals which come laden with pollen from another flower, it is unavoidable that foreign pollen should be deposited on the stigma, and so a crossing results. The same is true of various Boraginaceæ (e.g. *Echium*), Scrophulariaceæ (e.g. *Pæderota Ageria*), Bindweeds (e.g. *Convolvulus sepium*, *sylvaticus*, *vucanus*), Caprifoliaceæ (e.g. *Linnæa borealis*), Rhododendrons (e.g. *Rhododendron Chamæcistus*), and Cactaceæ (e.g. *Mammillaria*, *Echinocactus*). Many flowers whose entrance is directed upwards (e.g. *Lilium bulbiferum*, *Glaucium luteum*, *Gentiana Bavarica*, *nivalis*, *verna*) show the same condition of anthers and stigmas. In the flowers of the Mezereon (*Daphne Mezereum*) the stigma is not beyond and above the anthers, as in the plants just mentioned, but it forms the termination of the ovary at the base of the perianth-tube, whilst the anthers are situated in the upper part of the tube. Some pollen may occasionally fall from the anthers on to the stigmas in erect flowers, especially when they shrivel

up as the blossom fades, but the majority of *Mezereon* flowers stand out horizontally from the branches, and in these it is hardly possible for the adhesive pollen to reach the stigmas unaided, although the anthers and stigma are not more than 2 mm. apart. *Mezereon* flowers are visited so industriously by bees, however, that most of the stigmas are pollinated by strange pollen, and thus manifold crossings are obtained. In the majority of Orchids, too, the pollen is only brought from its hiding-place by insects which hardly ever deposit it on the adjacent stigma, but as a rule transfer it to the stigma of another flower.

Heterostyled plants present a peculiar condition. Many *Gentianaceæ* (e.g. *Menyanthes trifoliata*, *Gentiana Rhaetica* and *Germanica*), the various species of Bastard Toadflax (*Thesium*), numerous *Primulaceæ* (e.g. *Androsace*, *Aretia*, *Gregoria*, *Hot-*

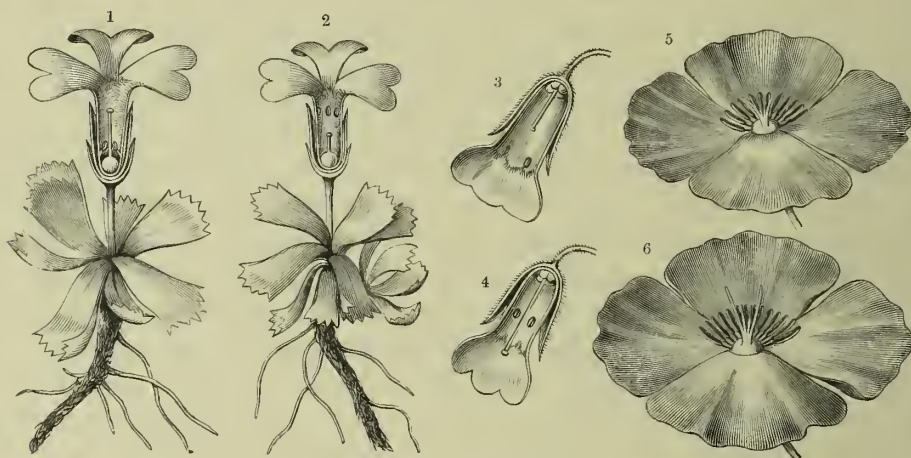


Fig. 288.—Heterostyled flowers.

<sup>1</sup> Plant of *Primula minima* with a long-styled flower. <sup>2</sup> Plant of the same species with a short-styled flower. <sup>3</sup> Short-styled flower of *Pulmonaria officinalis*. <sup>4</sup> Long-styled flower of *Pulmonaria officinalis*. <sup>5</sup> Short-styled flower of *Eschscholtzia Californica*. <sup>6</sup> Long-styled flower of the same plant. All nat. size.

*tonia*, *Primula*, see figs. 288<sup>1</sup> and 288<sup>2</sup>) as well as many *Boraginaceæ* (e.g. *Myosotis*, *Mertensia*, *Pulmonaria*; see figs. 288<sup>3</sup> and 288<sup>4</sup>) and members of other groups, bear flowers with relatively short styles on one plant, the anthers being above the stigma, while, on another plant of the same species, the flowers have all relatively long styles, and the anthers are inserted below the stigma. At the opening of the flowers the stigmas cannot receive pollen unaided either from the anthers above or from those below them. But an insect, which, by inserting its proboscis into a short-styled flower, has brushed against the anthers at the mouth of the corolla-tube, and thus loaded itself with pollen, will deposit this exactly on the stigma of a long-styled flower, should it enter one, since the stigma is just at the same level in the second flower as the circle of anthers in the first-visited, short-styled form. In the same way it is hardly necessary to say that the pollen, which has adhered to the proboscis of a honey-sucking insect half-way up the corolla-tube of a long-styled flower, will be deposited on the stigma which reaches the same level in a



short-styled flower. I shall return to the subject of heterostyly in the next chapter, and will merely say here that there are also plants whose anthers and stigmas present three kinds of arrangement. For example, in the Purple Loosestrife (*Lythrum Salicaria*) the flowers on one plant will have long styles, on another medium styles, and short styles on a third plant; the two whorls of stamens in plants with long-styled flowers are below the stigma; in the medium-styled flowers, one whorl of anthers is above, and the other below the stigma; whilst in the short-styled flowers both whorls of anthers are above the stigma. We should also briefly state here that the *Eschscholtzia*, which usually possesses four styles (figs. 288<sup>5</sup> and 288<sup>6</sup>), develops styles of unequal length in its flowers; in some flowers, which are distinguished by their larger circumference, there are two longer and two shorter. The longer styles receive the pollen from other flowers, and are adapted to cross-fertilization, while the shorter styles are pollinated by the anthers standing close beside them (fig. 288<sup>6</sup>). There are also smaller flowers containing four styles which are all so short that they do not project above the pollen-producing anthers (fig. 288<sup>5</sup>). We can only briefly touch upon the remarkable Ranunculaceæ and Rosaceæ (*Anemone baldensis*, *Pulsatilla alpina*, *vernalis*, *Ranunculus alpestris*, *glacialis*, *Geum montanum*, *reptans*, &c.) which develop pseudo-hermaphrodite male flowers, as well as two kinds of hermaphrodite flowers, those with large ovary and few short stamens, and those with small ovary and numerous long stamens; but it may be stated that the former are adapted to crossing, and the latter to autogamy.

Another contrivance for promoting cross-fertilization is the interchange of position of anthers and stigmas. Although this has been repeatedly mentioned already (see pp. 250 and 276), it must again be described, since it represents one of the most important contrivances for the crossing of hermaphrodite flowers, and can only be completely understood when regarded from this point of view. The change of position consists essentially in this; the place occupied for some time by the ripe stigma is assumed later by the pollen-laden anthers, and *vice versâ*. Since this position is directly in the path traversed by the honey-sucking insect as it enters, the pollen is brushed on to the stigmas in one flower and collected from the anthers in another—a condition necessarily leading to cross-fertilization. This change of position is brought about by spontaneous movements in the anther-filaments, or by similar changes of direction in the styles. It may even happen that both the stamen-filaments and the styles of the same flower alter their position and actually exchange places. We may distinguish no less than *ten* different varieties of this change of position.

In one group of plants, of which the Dwarf Leek (*Allium Chæmæmoly*) may be taken as an example, the ripe stigma is seen in the middle of the newly-opened flower, while the anthers are pressed back against the perianth-leaves. Later, as the anthers open and expose their pollen, they pass towards the centre by reason of the peculiar movement of their filaments till they come close to the stigma and form a yellow ball. This is necessarily touched by an insect as it enters the

flower, although previously only the stigma would have been brushed in the same position.

In a second group, to which belong many Gentians (*Gentiana asclepiadea*, *ciliata*, *Pneumonanthe*), most Malvaceæ (*Abutilon*, *Malva*), the numerous species of Monkshood (*Aconitum*), *Funkia*, and the Red Valerian (*Centranthus*), the pollen in a young flower is exposed close to the path of the honey-seeking insect; sometimes only from a single anther (as in *Centranthus*, figs. 289<sup>1,2,3</sup>), sometimes from five or six, or from quite a number united together in one bundle (Malvaceæ). The stigmas are at first hidden behind, *i.e.* below the anthers; later on the anther-filaments bend back in a semicircle, and the stigmas are exposed. When only a single stigma is present (hitherto hidden behind the anther as in *Centranthus*) of course only one can be displayed (see figs. 289<sup>2</sup> and 289<sup>3</sup>). When an insect comes for honey it strikes against the exposed stigmas, just as it did previously against the anthers.

The third group contains species of *Gladiolus*, *Acanthus*, Penstemon, and Sage (*Salvia*; see fig. 271, p. 262). The styles and stigmas of the horizontally-directed flowers of these plants lie close against the roof-like portion of the corolla above the anthers, but later the style bends down until the stigma lies just in the path which leads to the honey, so that insects passing this way (laden with pollen from the younger flowers) deposit it in older ones, so producing cross-fertilization.

In the fourth group, to which belong the genera *Allionia* and *Phalangium*, the stigma at the commencement of flowering is at the end of the projecting style in front of the anthers, and insects flying to the flowers are obliged to brush against this stigma. Afterwards the style bends sideways through an angle of 80–90°, so that the stigma is removed from the road leading to the honey. Now, when insects fly to the flower they come in contact with the pollen-covered anthers only.

In flowers of the fifth group, of which the Germander (*Teucrium*; see figs. 289<sup>4,5,6</sup>) is a type, the change of position resembles that of *Centranthus* in that the thread-like anther-filaments are placed at the aperture of the flower, so that insects strike against the anthers as they enter. Afterwards the stamens bend up, and the anthers are removed from the path, whilst concurrently the stigmas are exposed. But there is this important difference—in the Germander the style as well as the stamens alters its direction and position and bends downwards like a bow till the stigmas come to lie in exactly the same position as was previously occupied by the anthers.

In the flowers of the sixth group, typical examples of which are furnished by the sweet Basil (*Ocimum Basilicum*) and the well-known climber, *Cobaea scandens*, the same kind of change of position occurs as in the Germander; but the stamen-filaments bend down instead of up, and the style upwards instead of downwards. At the beginning of flowering the anthers intercept the passage to the honey at the base of the flower, but later on they sink downwards, while the style arches up, bringing the stigma to the identical place previously occupied by the anthers.

The remarkable change of position of stigmas and anthers in plants of the

seventh group as shown by the Nightshade (*Atropa*), *Scopolia*, Henbane (*Hyoscyamus*) and the Mandrake (*Mandragora*) has been already described on p. 278 and illustrated in figs. 279<sup>8</sup> and 279<sup>9</sup>. In young blossoms the stigma stands in the middle of the flowers, and the anthers lie against the walls of the corolla: in older flowers the anthers stand in the middle, and the style becomes pressed against the corolla.

The shrubby species of Honeysuckle (*Lonicera alpigena*, *nigra*, and *Xylosteum*), and the genus *Scrophularia* may be taken as examples of the eighth group. Their flowers are horizontally placed. At first the straight style rises out of the centre of the flower, and the stigma is held directly in the path leading to the honey.

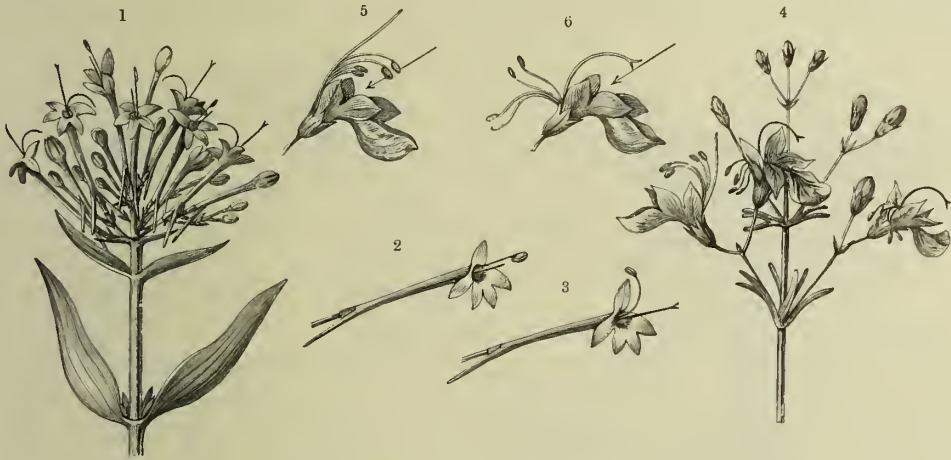


Fig. 289.—Change of Position of Anthers and Stigmas.

<sup>1</sup> Inflorescence of the Red Valerian (*Centranthus ruber*). <sup>2</sup> A single flower of the Red Valerian shortly after opening. <sup>3</sup> The same flower at a later stage. <sup>4</sup> Inflorescence of *Teucrium orientale*. <sup>5</sup> Single flower of the same plant shortly after opening. <sup>6</sup> The same flower at a later stage. <sup>1</sup> and <sup>4</sup> nat. size; <sup>2</sup>, <sup>3</sup>, <sup>5</sup>, and <sup>6</sup> somewhat magnified.

The anthers are above the stigma in *Lonicera*, but in *Scrophularia* they are hidden at the end of their arched filaments in the cavity of the pitcher-shaped corolla. Later on the stigma is moved out of the path by the downward curvature or sharp bending of the style, the anthers assuming the position occupied by the stigma by means of a corresponding straightening and alteration of direction of their filaments.

The Hellebore (*Helleborus*), a type of the ninth group, has comparatively large flowers with abundant honey. The honey is not in the centre of the flower, as in the instances quoted above, but is secreted in cornet-shaped receptacles outside the ring of stamens. Accordingly the honey-sucking insects do not go to the centre of the flower but to the circumference, and this explains why the stigmas and anthers, which are to be brushed by the insects, are arranged in a corresponding circle. When the flower opens the styles radiate outwards, and are bent, so that the stigmas stand over the honey receptacles. The anthers are crowded together in the middle of the flower, and are not touched by the insect as it enters. Afterwards the styles straighten and move towards the centre of the flower while the stamen-filaments



elongate, and thus assume a position overhanging the honey receptacles, where they are inevitably brushed by insects.

For the tenth group we may select the Rue (*Ruta*; see fig. 290) as an example. The flower contains ten anthers supported by stiff filaments, arranged in the form of a star. First, one of these filaments bends up and places its anther in the middle of the flower, just in the way to the fleshy ring which secretes nectar at the base of the pistil: it remains there about a day, and then bends back and resumes its former position. While the first stamen is bending back, a second rises up and undergoes the same movements. And so it goes on until the ten anthers have all stood in the centre of the flower in turn and discharged their pollen there. When, finally, the last stamen has bent back again, the stigma, which has meanwhile matured, is seen in the centre of the flower where the anthers have successively shed their pollen.

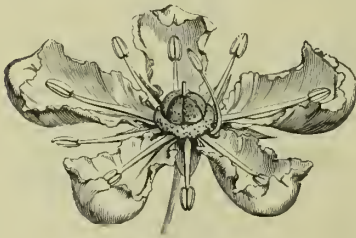


Fig. 290.—Flower of the Rue (*Ruta graveolens*)  $\times 3$ . (After Baillon.)

A process which is closely connected with the interchange of position of anthers and stigmas, in bringing about cross-fertilization between hermaphrodite flowers, is the separation and subsequent falling away of the stigmas when the surrounding anthers begin to dehisce. We may take one of the Urticaceæ, the Wall Pellitory (*Parietaria*; see figs. 291<sup>2, 3, 4</sup>), as a type of this. The stigma is always developed before the flowers open in this

plant, and at the commencement of the flowering period it may be seen projecting like a dusting-brush from the green flower-bud (fig. 291<sup>3</sup>). The curved anther-filaments are at this time coiled like watch-springs and covered over by the as yet unopened floral-leaves. Before these filaments jerk up and scatter their pollen the stigma withers and shrivels up and the style becomes detached from the ovary. It falls off with the dried-up stigma, so that, when the pollen is liberated from the anthers, the ovary is terminated merely by a small stump which is really the withered remnant of the fallen style (fig. 291<sup>4</sup>).

The falling of the anthers and stamens at the time when the adjoining stigmas become mature is of much more frequent occurrence than the detachment and falling of the stigmas before the pollen is shed. In the flowers of Balsams (*Impatiens glandulosa*, *Nolitangere*, *tricornis*, &c.) the anthers are united into a kind of cap which arches over the stigma. As soon as the flower has opened and become accessible to flying insects, the anthers dehisce and only the cap which they form can be seen at the entrance to the flower. Later, the filaments of the anthers become detached, and the anther-cap falls out of the flower; only the stigma, which has meanwhile matured, is now visible in the middle of the flower. The large-flowered species of Crane's-bill (e.g. *Geranium argenteum*, *pratense*, *sylvaticum*; see fig. 291<sup>1</sup>) have a similar arrangement. Two of the anthers which have hitherto been covered by the petals dehisce almost simultaneously with the opening of the flower; the others then open in a certain order and expose their pollen in

turn. The stigmas in the centre of the flower are still folded together: as soon as they begin to separate the anthers fall away from their filaments, and the five mature outspread stigmas are surrounded only by the needle-shaped filaments minus their anthers (fig. 291<sup>1</sup>, the left-hand flower). The same thing happens in some Saxifrages, of which *Saxifraga rotundifolia* (fig. 292) will serve as a type. After the petals have unfolded, a peculiar action on the part of the stamens is to be observed for several days. Each anther as it dehisces is raised up by its filament into an erect position (see fig. 292<sup>2</sup>), but remains in this position only for a short time; it bends down again the next day or the next but one, resuming its original position. The anther falls off, or if it remains as a shrivelled mass on the top of the filament it has by this time lost all its pollen. All the stamens in succession



Fig. 291.—Completely dichogamous Flowers.

<sup>1</sup> *Geranium sylvaticum* with completely protandrous flowers. <sup>2</sup> *Parietaria officinalis* with completely protogynous flowers.

<sup>3</sup> Single flowers of *Parietaria* with mature brush-shaped stigma and closed coiled-up stamens. <sup>4</sup> The same flower at a later stage of development; the stigma has fallen off, the filaments have straightened, and the anthers are flinging out their dusty pollen. <sup>1</sup> and <sup>2</sup> nat. size; <sup>3</sup> and <sup>4</sup> somewhat magnified.

undergo this rising and sinking. Not until all the pollen has disappeared do the two short styles, which up till now have been folded together like the two ends of a pair of tongs (fig. 292<sup>2</sup>), separate from one another, and their stigmas become capable of pollination (fig. 292<sup>3</sup>). The Grass of Parnassus (*Parnassia palustris*; see fig. 267<sup>4</sup>, p. 249) as well as many Caryophyllaceæ (e.g. *Alsine verna*, *Silene Saxifraga*), many Valerians (e.g. *Valeriana officinalis*) and Tulips (e.g. *Tulipa Didieri*) exhibit the same course of development, especially the falling away of the anthers. In Caryophyllaceæ it often happens that the antherless filaments bend down in a semicircle under the petals and become so hidden that the flower might at first sight be thought to be pistillate instead of truly hermaphrodite.

The end gained by this shedding of the anthers in the Balsam, Saxifrage, Grass of Parnassus, Chickweed, Pink, and numerous other plants with hermaphrodite flowers, is also obtained in the following manner:—The anthers are covered over

and hidden by the petals as soon as the neighbouring stigma begins to mature, so that they are no longer able to shed their pollen. The consequence is that the stigmas can only be pollinated with foreign pollen, which is of course the same thing as saying that only cross-fertilization can occur in these hermaphrodite flowers. In the hermaphrodite flowers of the Spiderworts (*Tradescantia crassula*, *Virginica*, &c.), the anthers dehisce a considerable time before the stigmas mature. When the flower first opens, therefore, pollen only can be removed. But as soon as the stigmas become capable of fertilization the stamens roll up in a spiral, and soon afterwards the perianth withers and forms a moist, pulpy mass, quite covering the anthers on their rolled-up filaments. The style still projects stiffly from the flower and the stigmas remain capable of fertilization the whole of the following day. Small flies and other insects with short probosces now visit these flowers to suck up the juice of the pulpy petals, and at the same time the stigma is pollinated with



Fig. 292.—Dichogamy in *Saxifraga rotundifolia*.

<sup>1</sup> A portion of the inflorescence with flowers at different stages; that to the right still young, in the middle older. <sup>2</sup> Longitudinal section through a single flower with folded stigmas and one stamen shedding its pollen. Another stamen (to left of pistil) has lost its anther, and four others have anthers which have not yet dehisced. <sup>3</sup> The same flower at a later stage of development, with mature stigmas. <sup>1</sup> nat. size; <sup>2</sup> and <sup>3</sup>  $\times 4-5$ .

pollen which they have brought from distant flowers, it being impossible to obtain that of the neighbouring anthers. It is an odd fact that some of the flowers of a *Tradescantia* plant, all of which opened simultaneously in the morning, will be already closed the same evening, whilst others will remain open the whole of the following day. It would seem that in those flowers which remain open the succulent hairs of the staminal filaments are devoured by flies, thus is the pollen obtained which is to be taken to the stigmas of the flowers whose anthers are hidden under the pulpy perianth. A peculiar process is observed in the flowers of *Telephium Imperati*, a native of Southern Europe, belonging to the Caryophyllaceæ. Here the anthers open first, but, as soon as the stigmas mature, the anthers—even if they have not as yet discharged all their pollen—are covered over by the petals, so that only pollen from other younger flowers can reach the ripe stigmas.

By these contrivances the same result is obtained in hermaphrodite flowers as by the separation of the two kinds of sexual organs on different plants, or on different flowers of the same plant. In all cases it seems to be the separation of the two kinds of sexual organs within the limits of the same species which is aimed at. The separation of the two kinds of sexual organs by the non-simultaneous maturation of the pollen and of the stigmas in any one species is just as effective in



promoting cross-fertilization as their separation by actual distance. In other words, separation in time is as efficient as separation in space; and these flowers, though structurally hermaphrodite (in that they contain both male and female organs), are—as the mechanism works out—unisexual (in that only one set of organs is mature at any given moment). This maturation of the sexual organs so that they are capable of fertilization at different times in the same plant, is termed *dichogamy*



Fig. 293.—Incompletely dichogamous Flowers.

<sup>1</sup> *Epilobium angustifolium* with protandrous flowers. <sup>2</sup> *Eremurus Caucasicus* with protogynous flowers.

(δίχα, apart, and γάμος, marriage), and we may distinguish between *protogynous* and *protandrous dichogamy*. If the stigmas are able to receive pollen, retain it, and stimulate it to put out pollen-tubes at a time when the pollen in the same flower is still unripe and hidden in the anthers, this particular species is termed *protogynous* (from πρῶτος, first, and γυνή, a woman). But if the pollen is shed from the dehiscent anthers, whilst the stigmas in the same flower are yet immature, *i.e.* not susceptible to pollination, then the species is said to be *protandrous* (πρῶτος, first, and ἀνὴρ, a man). In the racemose inflorescence of the Willow-herb (*Epilobium angustifolium*), which is represented in fig. 293<sup>1</sup>, the upper flowers are seen to be still closed; a little lower are three flowers which have just opened, the middle one being visited by a

humble-bee, whilst lower still are flowers which have been open for two days. In the recently-opened flowers the anthers are covered with pollen, while the stigmas on the end of the downwardly-curved style are as yet immature and folded together into a club-like body. This plant is therefore protandrous. The inflorescence of *Eremurus Caucasicus*, belonging to the Liliaceæ, is figured beside it (293<sup>2</sup>). Here, again, the youngest flowers are still in bud, those coming next below have just opened, whilst lower down still are the oldest flowers of all. In the newly-opened flowers the anthers are closed and no pollen is exposed, but the pointed stigma, terminating the upwardly-curved style, is already mature, so that this plant is protogynous. Both protandrous and protogynous dichogamy may be complete or incomplete. It is *complete* when the stigma begins to ripen after the removal of the pollen from the adjoining anthers by wind or by flower-visiting insects, so that it can no longer fertilize its own flower; or if the stigma is withered, dried up, or fallen away as soon as the anthers of the same flower open and expose the pollen or scatter it abroad, as in the Wall Pellitory (see figs. 291<sup>2,3,4</sup>). Dichogamy is *incomplete* when the ripening of the two kinds of sexual organs is not, indeed, simultaneous, but when the capacity for fertilization of one sex is not at an end before the other sex in the same flower is mature. There are, of course, many grades in incomplete dichogamy. In long-lived flowers the start which one sex has over the other may amount to several days, but in short-lived flowers it may be limited to a few hours. Cruciferæ all have protogynous flowers. The already mature stigma is visible in the centre of the flower as soon as the petals open, but the surrounding anthers are still shut up. This only lasts for a short time; soon the anthers dehisce, and then both sexes come into operation. In *Lepidium Draba*, *Sisymbrium Sophia*, and numerous other species, this difference of time (lasting from the moment when the stigma is accessible to the moment when the anthers begin to shed the pollen) is only 2-5 hours. The same may be said of numerous Rock-roses, Papaveraceous plants, Cactuses, Ranunculaceæ, Rosaceæ, Boraginaceæ, Gentianaceæ, Ericaceæ, and Valerianaceæ (e.g. *Helianthemum alpestre*, *Glaucium luteum*, *Opuntia nana*, *Actæa spicata*, *Adonis vernalis*, *Atragene alpina*, *Clematis Vitalba*, *Potentilla caulescens*, *Cynoglossum pictum*, *Lithospermum arvense*, *Menyanthes trifoliata*, *Arctostaphylos uva-ursi*, *Vaccinium Myrtillus*, *Valerianella dentata*). Even the majority of ephemeral flowers exhibit dichogamy. The flowers of the Marvel of Peru (*Mirabilis Jalapa*) open between seven and eight o'clock in the evening; as soon as the margins of the flower unfold, the small stigma, resembling a tiny brush, is able to receive pollen, but the anthers are as yet entirely closed. About 10-15 minutes later the anthers dehisce and shed their pollen. The difference in the time is so slight here that it would be unnoticed by most people, and this explains why such flowers have not been regarded as dichogamous. But the very circumstance that the maturation of the two kinds of sexual organs is not simultaneous, even in ephemeral flowers, is of the greatest importance for the question of the significance of dichogamy and must be especially dwelt upon here.

In protogynous dichogamy it is no uncommon thing for the stigma to project from the flower already fitted to receive pollen whilst the petals are still closely shut, the whole flower having the appearance of a bud. This happens in the Curled Pondweed (*Potamogeton crispus*, figured on p. 148), in Asphodels (e.g. *Asphodelus albus*), in Woodrushes (e.g. *Luzula nivea*), in Elms (e.g. *Ulmus campestris*), in the Plantain (e.g. *Plantago media*), in several Rhododendrons (e.g. *Rhododendron Chamæcistus*), in *Cortusa*, *Deutzia*, and many other plants. On the other hand, many plants with protandrous dichogamous flowers are known where the pollen is shed from the anthers while the petals are still folded as in the bud. On opening the ripe bud of *Crucianella stylosa* (figured on p. 265), it can be seen at a glance that the anthers have already dehisced some little time, and have deposited their pollen under the dome of the closed bud on the thickened warty surface at the end of the style. In the flowers of *Rhododendron hirsutum*, the pollen falls from the anthers while still in the bud, and the same may be observed also in many Composites, Campanulaceæ, and Papilionaceous flowers.

We are not yet in a position to say whether protandrous or protogynous species are the more abundant, although the dichogamy of thousands of plants has been investigated. By generalizing on this subject one is liable to fall into very great error. It would be particularly dangerous to generalize prematurely on the results which have been obtained from the examination of many species of a genus, or many genera of a family, and to consider them to hold good for the whole group, for most genera contain some protandrous species, even when the majority of them are protogynous, and *vice versâ*. Liliaceous plants are described as protandrous in most Botanical books, but in reality many of the genera and species are incompletely protogynous (*Amaryllis*, *Asphodelus*, *Colchicum*, *Erythronium*, *Leucojum*, *Lilium Martagon*, *Narcissus poeticus*, *Ornithogalum umbellatum*, *Scilla*, *Trillium*, &c.). Among the Umbelliferae, which are usually stated to be all protandrous, there are quite a number of protogynous genera and species, as, for example, *Aethusa*, *Astrantia*, *Caucalis*, *Eryngium*, *Hacquetia*, *Pachypleurum*, *Sanicula*, *Scandix*, and *Turgenia*. This also applies to the Saxifrages: the majority, of course, are protandrous, but some of them, viz. *Saxifraga androsacea* and *peltata* are decidedly protogynous. The large-flowered species of Crane's Bill (*Geranium argenteum*, *lividum*, *pratense*, *sylvaticum*) are protandrous, the small-flowered (*Geranium columbinum*, *lucidum*, *pusillum*, *Robertianum*) are protogynous. In the Scrophulariaceæ the genera *Digitalis* and *Penstemon* are protandrous, and the genera *Linaria*, *Pæderota*, *Phygellus*, *Scrophularia*, *Veronica* protogynous. Of species belonging to Boraginaceæ some are protandrous (e.g. *Borago*, *Echium*), others protogynous (e.g. *Cynoglossum*, *Lithospermum*). In Ranunculaceæ the genus *Aconitum* is protandrous, while the genera *Adonis*, *Anemone*, *Atragene*, *Clematis*, and *Pæonia* are protogynous. In the Gentian family some are protandrous, viz. *Swertia perennis*, *Gentiana asclepiadea*, *ciliata*, *cruciata*, *Frælichii*, *Pannonica*, *Pneumonanthe*, *punctata*, and *prostrata*; others, especially *Menyanthes trifoliata*, *Gentiana Bavarica*, *Germanica*, *glacialis*, *Rhetica*, and *verna* are



protogynous. The same is true of Ericaceæ, Valerianaceæ, Polemoniaceæ, and many other groups. As far as we know, the Composites, Campanulaceæ, Labiataæ, Malvaceæ, Caryophyllaceæ, and Papilionaceous plants are exclusively protandrous, Rushes and Woodrushes (*Juncus* and *Luzula*), Aristolochiaceæ and Thymelaceæ, Caprifoliaceæ, Globularias, Solanaceæ, Rosaceæ, Berberidaceæ, and Cruciferae exclusively protogynous.

It has already been pointed out that the non-simultaneous maturation of the sexual organs goes hand in hand with the separation in space of the two sexes in most instances, or, in other words, that in plants where the two kinds of sexual organs have in any way been separated from one another in the flowers by actual distance, dichogamy also obtains. Thus, for example, it appears that all species of plants whose hermaphrodite flowers are adapted to cross-fertilization by the relative position and arrangement of their two kinds of sexual organs, or by the interchange of position of anthers and stigmas are, moreover, dichogamous, although this dichogamy may be only of slight duration. Plants with heterostyled flowers are also dichogamous, since those with short-styled and those with long-styled flowers develop at different times. If one observes the many hundred individuals of *Primula Auricula*, growing side by side on a rocky crag under the same conditions, it is easy to see that the plants with long-styled flowers are earlier than those with short styles. The former are already over while the latter are in full bloom. The reverse is the case in *Auricula longiflora*; here plants with short-styled flowers are in full blossom when the long-styled flowers of the neighbouring plants are still in bud.

Plants bearing pseudo-hermaphrodite flowers are also dichogamous. The Valerians (*Valeriana dioica*, *polygama*, and *tripteris*) open their pistillate flowers 3-5 days before their staminate flowers in the same locality; these plants are therefore decidedly protogynous. In the Alpine Dock (*Rumex alpinus*), the stigmas of the pistillate flowers are ripe 2-3 days before the anthers of the staminate flowers and of the truly hermaphrodite flowers on the same plant have opened. In the Ash (*Fraxinus excelsior*), the stigmas of the pistillate flowers are mature whilst the anthers in the neighbouring staminate and hermaphrodite flowers are still closed. The latter do not usually shed their pollen till 4 days later. The dichogamy of the Grasses, which bear both true staminate and hermaphrodite flowers, is very striking (e.g. *Anthoxanthum odoratum*, *Hierochloa australis*, *Melica altissima*, and *Sesleria cœrulea*). In these plants the anthers do not liberate their pollen until the neighbouring stigmas have been mature for two days. This may also be observed in Composites whose capitula contain true hermaphrodite and pistillate flowers, and in those with true pistillate and pseudo-hermaphrodite male flowers. The stigmas of the pistillate flowers are already mature two days before any pollen can be obtained from the adjoining truly hermaphrodite or staminate flowers. It will suffice to mention as examples of this *Aster alpinus*, *Aronicum glaciale*, *Bellidiastrum Micheli*, *Doronicum cordatum*, *Erigeron alpinus*, *Gnaphalium Leontopodium*, *Tussilago Farfara*, and *Calendula officinalis*.

*nalis*. Labiates which bear only true hermaphrodite flowers on one plant, and only pseudo-hermaphrodite female flowers on another are protogynous. In the Marjoram (*Origanum vulgare*), the pistillate (pseudo-hermaphrodite female) flowers are ripe as much as eight days or longer before the true hermaphrodite flowers. The fact must be emphasized that these remarks only refer to such flowers or plants as develop under similar conditions of life, and that they are not applicable to instances where the early or late maturity depends upon whether the habitat is a sunny or shaded one.

As far as we can tell at present all monœcious plants are protogynous. Sedges, Bulrushes, Bur-Reeds (*Carex*, *Typha*, *Sparganium*), Aroids with monœcious flowers, the Maize (*Zea Mays*), the monœcious Stinging Nettle (*Urtica urens*), the Water Milfoil (*Myriophyllum*), the Burnet (*Poterium*), the Burweed (*Xanthium*), the monœcious Euphorbiaceæ (*Euphorbia*, *Ricinus*, *Buxus*), and especially Alders and Birches, Walnuts and Planes, Elms and Oaks, Hazels and Beeches, are all markedly protogynous. In most of these plants, especially the last-named trees and shrubs, the dust-like pollen is not shed from the anthers until the stigmas on the same plant have been matured 2-3 days. Sometimes the interval between the ripening of the sexes is still greater. The majority of diœcious plants also are protogynous. In the luxuriant Willows on the banks of rivers a single species is sometimes represented by thousands of bushes. Some of them bear staminate, the others pistillate flowers. They grow on the same soil, are exposed to the same amount of sunlight, and are fanned by the same breezes, and yet, in spite of identical external conditions, the plants with pistillate flowers certainly precede their staminate neighbours. The stigmas of the Almond Willow (*Salix amygdalina*) are already mature 2-3 days before a single anther of this species has dehisced anywhere. The same happens in the Purple-willow, Osier, and Crack-willow. This phenomenon can also be observed in the sub-alpine Willows (*Salix herbacea*, *retusa*, *reticulata*), but here the difference in time is usually restricted to a single day. Among the countless plants of Hemp (*Cannabis sativa*), which grow up together in the summer in closest proximity from seeds sown on level fields, most of the individuals which bear pistillate flowers have already protruded their stigmas before a single staminate flower has opened. The latter do not unfold until 4-5 days after the pistillate plants have begun to blossom, and then only does the wind scatter the pollen from their versatile anthers. In the Dog's Mercury, especially in the perennial species of the genus (*Mercurialis ovata* and *perennis*) which grow in small clumps in the depths of our woods, plants with pistillate and others with staminate flowers being close together on the same soil, the stigmas are capable of fertilization at least two days before the pollen is shed. The same thing is observed in the Hop (*Humulus Lupulus*), and in many other diœcious plants.

All these facts are of the greatest importance in the question of the significance of cross-fertilization. If the maturation of the sexes at different times had been observed only in those species of plants which bear hermaphrodite flowers, dichogamy might be regarded merely as the completion of the contrivances for preventing

the pollen from fertilizing the stigmas of the same flower, *i.e.* for preventing self-fertilization or autogamy. For example, the relative position of the anthers and stigmas in the flowers of the Arrow-grass (*Triglochin*; see fig. 237, p. 149) renders it almost impossible for the pollen to reach the stigmas in the same flower, but the possibility would not be excluded were the anthers to shed their pollen at the time when the stigmas were capable of being fertilized. Since, however, in the flowers of the Arrow-grass, the stigmas are quite dried up at the time of dehiscence, autogamy is quite impossible, and so far dichogamy is a completion of the contrivances mentioned. But such cases of complete dichogamy as in the Arrow-grass, the Wall Pellitory, and the Grass of Parnassus, &c., are comparatively rare, and this explanation will not hold for the great bulk of hermaphrodite flowers which are incompletely dichogamous. Still less will it apply to monœcious and diœcious plants. Here there is no question of autogamy or self-fertilization, and for this reason all hypotheses founded on the prevention of self-fertilization by dichogamy are futile.

We cannot suppose, however, since the non-simultaneous maturation of the sexes is a phenomenon which occurs in most—perhaps in all—plants, that this contrivance has no meaning. I will now endeavour to elucidate the significance of dichogamy and invite the reader, first of all, to enter one of the Willow plantations which have been briefly described above. The Purple Willow (*Salix purpurea*) is just beginning to bloom. The pistillate flowers already display mature stigmas; but the staminate flowers are still behind, and not a single anther has opened. The staminate flowers of the Osier (*Salix viminalis*), on the other hand, growing in the same clump with the Purple Willow, are in their prime. The pollen of the Osier is to be had in any abundance. Numerous bees have been attracted by the scent and colour of the male catkins, and they buzz from bush to bush, sucking the honey and collecting pollen. They are not dainty in their work, and do not limit themselves to one species but fly impartially to the Purple Willow, to the Osier, or to other species of Willow which may happen to be present. Now, if a bee comes to suck the honey from the pistillate flowers of the Purple Willow, after it has just visited another Willow bush, where it has covered itself with pollen, obviously that bush must have been the Osier, Sweet Willow, Sallow Willow, or some other species, whose staminate flowers have already developed so far as to render their pollen accessible. It cannot have been a Purple Willow, because not a single anther of this species in the whole neighbourhood has yet opened. But since the stigmas of the Purple Willow are thus fertilized by the pollen of the Osier, &c., hybridization occurs. Two or three days later, a legitimate crossing may take place, for, by this time the anthers of the Purple Willow will have protruded from the staminate flowers and opened widely, and abundance of pollen will be afforded to insects. These are not slow to visit the now accessible flowers, and they remove some of the pollen and transfer it to the stigmas of the same species which are still capable of being fertilized. Thus at the commencement of flowering hybridization is alone possible, and legitimate cross-fertilization cannot take place till some time later,



in consequence of the dichogamy of these Willows. This obviously applies to all other Willows, and generally to all dicecious plants whose flowers are incompletely protogynous.

In order to show that the same processes obtain in monœcious plants, I would ask the reader to accompany me to the edge of a moor where numerous monœcious Sedges (*Carex*) form the chief constituents of the vegetation. Widely different species grow in varied profusion side by side. Here at the margin of a dark pool *Carex acutiformis*, *filiiformis*, *riparia*, *vesicaria*, *paniculata*, there, on the marshy stretch close by, *Carex flava*, *canescens*, *glauca*, *Hornschuchiana*, and many others. These Sedges do not all blossom at the same time; one ceases to flower just when another is in its prime, and when, in a third sort, the flowers have just begun to fade. All monœcious Sedges are protogynous. The stigmas have been ripe 2-3 days, and have protruded far beyond their subtending bracts, so that it would seem natural that the pollen, wafted by the wind, would remain attached to them. But the anthers of the staminate flowers of the same species have not yet opened. It is evident then that the stigmas must be pollinated during the first and second day with pollen from other species which blossom earlier, for since the anthers of these earlier species are already open, each gust of wind will shake out their pollen and blow it over the moor, pollinating everything which is capable of being pollinated. The pollen of the same plants (afterwards shed from the staminate flowers above and close to the mature stigmas) can only be received in the second place on account of its later arrival. Thus, we see that incomplete dichogamy promotes hybridization in the first place, and then, only later, a legitimate cross-fertilization in plants with monœcious flowers.

It is well known that all the plants of a species growing under similar external conditions do not blossom on the same day, and this fact is worth noticing in so far as it might be thought possible for the earlier plants of a species to provide pollen for the stigmas of later plants. This is certainly often the case, but it is also certain that the stigmas of the very earliest plant of a protogynous species can only be, and actually are, fertilized with pollen from another species which flowers still earlier; thus the conclusion already arrived at must remain unaltered.

It may be taken for granted, since plants with pseudo-hermaphrodite flowers behave exactly like dicecious and monœcious flowers in the manner of the transfer of their pollen, that their dichogamy has the same significance. The spikes of Docks belonging to the group *Lapathum*, viz. *Rumex alpinus*, *nemorosus*, and *obtusifolius*, bear principally pseudo-hermaphrodite flowers, which are some of them male, some female, and besides these a few true hermaphrodite flowers. In any one plant, the development of the stigmas is always considerably in advance of that of the anthers. The stigmas are ripe whilst the anthers are still closed. Under these circumstances the first flowers of a plant, whether pseudo- or truly hermaphrodite, can only receive pollen from other plants which have been in bloom for several days, and whose dehiscent versatile anthers have been robbed of their pollen by the wind. It may further be taken for granted that any hundred plants of *Rumex obtusifolius*,

growing together in a clump, will not all blossom together, and consequently innumerable crossings take place between the flowers of the individuals of this same species. The first ripe stigmas of the earliest plants of *Rumex obtusifolius* within an hour's walk can only receive their pollen during the first two days from other species of Dock, and therefore, when they first blossom, hybridization only can occur. It has already been stated that plants of Marjoram (*Origanum vulgare*, a Labiate), which bear pseudo-hermaphrodite female flowers, blossom fully eight days before those with truly hermaphrodite flowers. To this we might add that the plants which blossom first in any given district cannot obtain pollen from the same species, and that consequently, if the stigmas are, nevertheless, pollinated by insects, the pollen must have been obtained from some other species. In Compositæ, whose capitula contain both truly hermaphrodite and pseudo-hermaphrodite female flowers, the latter always mature some days before the former, and consequently the pioneer flowers in a given locality can only obtain pollen from species which bloom still earlier, so that again hybridization occurs. In the floral region of the Black Sea many Fleabanes grow side by side (*Inula Oculus-Christi*, *ensifolia*, *Germanica*, *salicina*, &c.), and in the summer they blossom in definite succession, so that one species always begins to fade when another is in its prime. Each capitulum of these Inulas consists of tongue-shaped pseudo-hermaphrodite female flowers on the circumference and tubular hermaphrodite flowers in the centre. The former unfold earlier than the latter, and for each species there is a certain period, if only two days, when the pollen, brought by insects to the stigmas of the pistillate flowers on the circumference, can only have been obtained from another species, since their own pollen is not obtainable. Many other examples of the same kind might be quoted, all pointing to the fact that hybridization at the commencement of flowering and the subsequent legitimate crossing depend mainly on the incomplete dichogamy obtaining in these plants.

It is the same with plants which have true hermaphrodite flowers. In heterostyled species either the long-styled or the short-styled flowers may develop first. The long-styled flowers of *Primula Auricula* and the short-styled flowers of *Primula longiflora* are the earlier, consequently, the stigmas of the first long-styled *Primula* plants can only be fertilized with pollen from other species. This is often actually effected by insect-agency, and gives rise to numerous *Primula* hybrids. The same thing is repeated in hermaphrodite flowers which are not heterostyled. When a plant is protogynous, as, for example, the open-flowered Pasque-flower, *Pulsatilla patens*, the earliest flowers can receive no pollen from anthers of their own species, because not one is open, but it would be possible for them to be provided with the pollen of other species of the same genus which inhabit the same locality but blossom earlier. This, of course, only holds good for the commencement of the flowering period, and only for those plants of the species which are the first to open their flowers in a given place. At a later period of flowering legitimate crossing will occur, because by that time the earliest plants have shed their pollen, and it may be collected and transferred by insects. Among hermaphrodite plants

there are many whose flowers are not protogynous but protandrous. Here the stigmas of the earliest flowers of a species cannot be pollinated, because they are immature and inaccessible. What, then, becomes of the pollen of these first protandrous flowers? If it is carried by the wind or by insects, as soon as it is liberated from the anthers, to any stigma, that stigma must of necessity belong to another species which has already become receptive. Towards the end of the flowering period, the pollen usually runs short in most protandrous species, whilst the stigmas of these stragglers have only just attained maturity. They could only obtain pollen from flowers which had not developed so far. But if these flowers are the last in the locality, and they are protandrous, there is no more pollen to be had from that species, and obviously they must be satisfied with pollen from some other. Accordingly hybridization is a matter of necessity in the latest flowers of hermaphrodite plants which are protandrous, just as it is in the earliest flowers of those which are protogynous.

From these facts we may infer that every dichogamous plant has an opportunity for illegitimate crossing or hybridization at the beginning or end of its flowering, and that dichogamy—especially incomplete dichogamy—is the most important factor in its production. Of course this does not exclude dichogamy from playing an important part in legitimate crossing as well. On the whole, however, we can maintain the view that the separation of the sexes by the maturation of the sexual organs at different times leads to hybridization, whilst their separation in space promotes legitimate crossing. The fact that the separation of the sexes in time and space usually occur in conjunction, harmonizes with this conclusion, *i.e.* that the dioecious, monoecious, and pseudo-hermaphrodite flowers, as well as those hermaphrodite flowers whose sexual organs are separated by some little distance, are in addition incompletely dichogamous, because by this contrivance the flowers of any species obtain (1) the possibility of hybridization at the beginning or end of their flowering period, and (2) of legitimate crossing during the rest of that time. This also explains why incomplete dichogamy is so much more frequent than complete dichogamy; why there are no dioecious species of plants with completely dichogamous flowers; and why, if one ever should occur, it would of necessity soon disappear. Let us suppose that somewhere or other there grows a species of Willow with completely protogynous dioecious flowers, that is to say, a species in which the female flowers mature first, and have ceased to be receptive before the male flowers in the same region discharge their pollen. Hybridization only could occur in it, and the young Willow plants resulting from it would all be hybrids whose form would no longer agree absolutely with that of the pistilliferous plant. The species would therefore not be able to reproduce its own kind by its seed, and it would leave no descendants of similar form; in other words, it would die out.

Two varieties of legitimate crossing, caused by the separation of the sexes by actual distance, have already been mentioned (see p. 301), viz., *Xenogamy* and *Geitonogamy*. We speak of xenogamy (from *ξένος*, a stranger, and *γάμος*, marriage) when the flowers in question belong to different individuals of the same species,



and of geitonogamy (from γείτων, a neighbour, and γάμος, marriage) when the two flowers are on the same plant. We cannot, however, draw a sharp line between the two. The offshoots of a plant, which become ultimately isolated, forming independent plants, are, in point of origin, identical with the branches of a plant which remain attached. Accordingly, when a crossing occurs between flowers produced on plants that have arisen from one another by offshoots, the process is not essentially different from the crossing which takes place between flowers on adjacent branches. It is nevertheless convenient to keep the two cases distinct, on account of certain processes connected with the greater or lesser distances between the flowers.

Both in xenogamy and geitonogamy the transport of the pollen is effected partly by wind and partly by flower-visiting insects. How this is carried out, and the endless variety which exists, has been dealt with in detail in previous chapters. Geitonogamy is not infrequently, however, brought about in other ways, as by the pressing of mature stigmas on the liberated pollen of neighbouring flowers, or by the actual falling of pollen upon them. Since these methods of cross-pollination have only been incidentally touched upon, they must be described here somewhat more fully.

The conditions for crossing between neighbouring flowers are simple when the flowers are crowded in heads, umbels, bunches, spikes, and the like, standing so close together that the stigmas of one flower can easily touch the pollen-covered anthers of another. And since this kind of crossing is actually very widespread and is repeated in certain species with great regularity, generation after generation, we are justified in regarding these forms of inflorescence as being particularly associated with geitonogamy, and in assuming that a not unimportant advantage of a crowded inflorescence lies in the possibility of crossing between the neighbouring flowers of a plant (see vol. i. p 740).

As we might expect, this particular form of crossing occurs with great frequency in Compositæ, whose flowers are crowded so densely into capitula that the whole inflorescence might be taken, at first sight, for a single flower; consequently this extensive family of plants, which includes more than 10,000 species, will be the most suitable in which to describe the phenomenon of geitonogamy. We will commence with those Composites whose heads only contain "ray" or ligulate florets. The term ray or ligulate floret is applied to florets whose corolla is tubular only at the base, the free end being flattened and projecting outwards like a tongue or strap, as in the Dandelion. In *Prenanthes* each capitulum consists of only five such ray-florets. In each floret the long, thin style is inclosed in a tube of anthers. The style is covered with stiff outwardly-directed bristles which are called "sweeping hairs". When the style elongates, immediately after the opening of the flower, these hairs sweep out the pollen which has been already shed into the interior of the anther-tube. The long style, rendered quite yellow by the pollen it carries, now projects from the empty tube of anthers. The two branches of the style which bear the stigmatic surface are at first folded together, but they soon separate, and the stigmas can then be fertilized by the aid of insects with pollen brought from

other plants, but not with that which lies on the sweeping hairs below the stigmas. As soon as the strap-shaped corollas begin to wither and shrivel, the two stylar branches diverge strongly, and twist and turn like tiny snakes sideways and downwards. At the same time adjacent styles come nearer to one another, and it is therefore natural that the stylar branches of neighbouring flowers should get entangled. In this way the stigmas of one flower (which are still in a receptive state) necessarily come in contact with the pollen on the sweeping hairs of another, and pollination ensues.

The same process occurs in the flowers of the Lettuce (*Lactuca*), the Alpine Sow-thistle (*Mulgedium*), and in *Chondrilla*, only here the heads contain more florets than in the form just described. The stylar branches do not undergo snake-like movements, but they diverge widely and roll back a little, an action altogether sufficient to bring them into contact with the styles of neighbouring flowers and to promote a crossing. It is worth noticing that the corollas of the ray-florets of *Prenanthes* roll outwards when they begin to fade, while those of the Lettuce and of the other Composites mentioned fold up and form a hood over the stylar branches during crossing. The Salsify (*Tragopogon*), Hawkweed (*Hieracium*), *Crepis*, *Scorzonera*, Hawkbit (*Leontodon*), Dandelion (*Taraxacum*), and many other Composites, of which these plants may be regarded as typical, contain in each head as many as 100 ray-florets arranged in spiral series (*cf.* fig. 222<sup>5</sup>, p. 112). The strap-shaped corollas separate in the morning and fold together in the evening, and similarly the anther-tubes and styles are inclined somewhat to the circumference of the capitulum in the morning, but come close together and assume an upright position in the evening. This gradual approach ultimately becomes actual contact, and since the development of the protandrous florets proceeds from the circumference towards the centre of the capitulum, the stigmas of the outer florets are mature at the time when the pollen has only just been swept out of the anther-tubes of the inner florets. The contact of the adjoining flowers, therefore, necessarily leads to cross-pollination. The fact that the corollas of the ray-florets in any capitulum are of unequal length (fig. 222<sup>5</sup>, p. 112) has also a close bearing on this process. If they were all equally long this contact and crossing would be impossible, for division walls would be interposed between the styles of the outer and inner florets. But the inner corollas are just short enough to allow the styles to touch one another. In many of these plants, *e.g.* in the Salsify (*Tragopogon*), geitonogamy is also assisted by the arrangement of the flowers in each capitulum, each flower of an outer row being placed exactly between two of the next inner series. When the capitulum closes, the two curved stylar branches of an outer floret, with their exposed stigmatic surfaces, become applied to the pollen-covered styles of the inner flowers immediately to right and left in front of them.

There are comparatively few species of Composites having exclusively tubular florets in which cross-pollination occurs between the members of the same capitulum. The most remarkable of these species belong to the Hemp Agrimony genus (*e.g.* *Eupatorium aromaticum* and *cannabinum*; see figs. 294<sup>1</sup> and 294<sup>2</sup>). The capitula

contain but few florets; those of *Eupatorium cannabinum* have five, which open one after another in the course of 5–8 days. Younger and older flowers are therefore always close together. The styles are rather different from those of other Composites, being divided almost half-way down into two long threadlike branches which bear the stigmatic tissue only on their lower portions. The rest of the branch is thickly studded with short bristles, the aforesaid sweeping hairs. The styles are parallel and folded together as long as they are inclosed in the anther-tube (see fig. 294<sup>2</sup>), and they remain closed for some time after they have elongated and

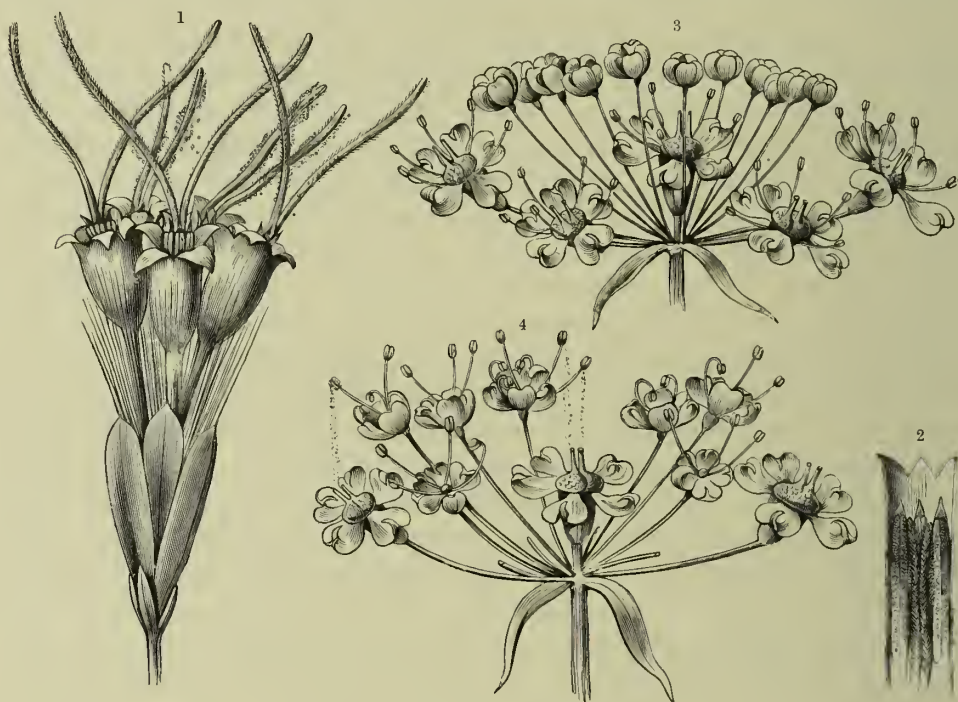


Fig. 294.—Geitonogamy with adherent pollen.

<sup>1</sup> Crossing of the stylar branches of neighbouring florets in the capitulum of *Eupatorium cannabinum*. <sup>2</sup> Longitudinal section through the upper part of a floret of *Eupatorium*; the two stylar branches are parallel and inclosed by the anther-tube, which is again surrounded by the corolla-tube. <sup>3</sup> Umbel of *Chærophylum aromaticum*; the truly hermaphrodite flowers are open, the pseudo-hermaphrodite male flowers are still closed. <sup>4</sup> The same umbel; the true hermaphrodite flowers have lost their pollen; the male flowers are now open, and their anthers drop pollen on the stigmas of the hermaphrodite flowers. All the figures somewhat enlarged.

pushed their way above the anthers. During the elongation the sweeping hairs brush the pollen from the anther-tube, and it then adheres in abundance to the outer side of each style-branch. This condition, however, does not continue for long. The stylar branches soon diverge at an angle of 40–50°. The branches of adjacent styles now cross one another like rapiers, and when the pollen is detached from the sweeping hairs it falls on to the mature stigmatic tissue. The closed pollen-covered stylar branches, as they emerge from the anther-tube, come in contact with the divergent branches of older neighbouring florets, and thus the pollen is transferred to the stigmatic tissue of the latter.



The capitula of the Colt's-foot (*Tussilago*) and of the Marigold (*Calendula*) contain two kinds of florets. In the centre are pseudo-hermaphrodite male flowers, whilst true pistillate ray-florets form the fringe of the capitulum. The latter open earlier than the disc-florets, and therefore at first can only be fertilized with pollen from other capitula which are further advanced. But soon the pollen is pushed out of the disc-florets of the same capitulum, and is deposited in a small clump at the top of the anther-tube. This pollen is conducted to the stigmas of the neighbouring ray-florets by different methods in the two genera mentioned. In the Colt's-foot the numerous ray-florets at the periphery are expanded horizontally during the daytime, but towards evening they fold up, and in this way, as they bend over the tubular florets, contact with their clumps of pollen is unavoidable. The pollen is transferred to the ray-florets, and when the capitula open again next morning, and the ray-florets bend outwards, the adherent pollen is freed, and slips down to the ripe stigmas at the base of the corolla. The process is far simpler in the Marigold. The stylar branches of the ray-florets are bent inwards over the adjoining disc-florets while the latter are still closed. When they open, and the pollen is swept out of their anther-tubes, it of course passes inevitably to the stigmas of the neighbouring ray-florets which are situated just above.

The Golden-rod (*Solidago*), Aster (*Aster*), and many other Composites classed together in the group of the Asteroideæ, closely resemble the Colt's-foot and Marigold in outward appearance, but their sexes are differently arranged. The tubular disc-florets are all truly hermaphrodite, and the outer ray-florets are truly pistillate. The latter mature first, and are adapted to hybridization, as we have already remarked. Two days later the hermaphrodite flowers of the disc open—those towards the circumference being the first. Their pollen is pushed out, and meanwhile the flowers bend slightly outwards, so that the pollen lying on the anther-tubes in the form of small clumps either comes into direct contact with the ripe stigmas of the marginal ray-florets or falls on to them from a short distance.

In very many Composites the capitulum contains only hermaphrodite flowers with tubular corollas. The development of the flowers again proceeds from the circumference towards the centre of the capitulum, and in each flower, soon after the corolla has opened, the pollen is swept and pushed out of the anther-tube by the sweeping hairs or warts on the outer side of the style. The pollen forms a small clump at the mouth of the anther-tube, but does not retain this position long. The two stylar branches which have hitherto been folded together (their outer surface being coated with pollen) soon separate and often bend back in a curve so as to expose their ripe stigmatic surfaces. The pollen is thus for the most part detached in small crumbling balls which simply tumble down. In this way they reach the ripe stigmatic tissue of the older neighbouring flowers and geitonogamy ensues. Various contrivances are met with in these Composites to prevent the pollen which falls from the younger flowers from missing its mark, and to ensure its arrival on the stigmas of the nearest older flowers. In *Homogyne alpina* (an alpine plant related to the Butterbur) the tubular florets on the flat receptacle of the

capitulum are of unequal length. The marginal florets are rather shorter than the central ones, so that the stylar branches of the former are lower than those of the latter. But this is not enough to bring the pollen which has fallen from the higher stylar branches on to the stigmatic tissue of these older lower ones—since the lower are situated rather nearer the circumference of the capitulum, and it is therefore necessary that the pollen-bearing styles should incline outwards if their pollen is to reach its proper destination. This is what actually happens. The originally straight and erect styles bend outwards at an angle of  $70-90^\circ$ , even before their branches have separated, and while they yet retain the pollen which they have collected from the anther-tubes. When it is thrown off, it thus unavoidably reaches the lower stigmas of the older flowers. Or sometimes it happens that the divergent stylar branches of the younger flowers with attached pollen come into direct contact with the stylar branches of older flowers, and that geitonogamy is effected in this way.

Numerous other Composites whose capitula are composed entirely of tubular hermaphrodite flowers exhibit the same processes as *Homogyne*, which has been chosen here as a type. The Wormwoods of mountain heights, e.g. *Artemisia Mutellina* and *spicata*, exhibit a slight deviation. In them the central florets are raised above the marginal ones, not only by their greater length, but because the receptacle on which they stand is considerably arched. Obviously the florets at the top of the dome will stand higher than those round its circumference. In very many Composites (e.g. in *Doronicum glaciale* and *scorpioides*, in *Senecio cordatus*, in *Telekia*, *Bupthalmum*, *Anthemis*, and *Matricaria*), the receptacle is at first flat or but slightly arched; but during the flowering period it rises up so much that it assumes the form of a hemisphere, or even of a cone. This elevation in *Doronicum*-capitula, for example, amounts to 1 cm., and it is relatively even more in species of *Anthemis* and *Matricaria*. The immediate consequence of this change in the receptacle is of course an alteration in the direction of the flowers which stand on it. Flowers which stood erect on the receptacle of the capitulum when it first opened, assume later an almost horizontal position. But the most remarkable thing is that these changes keep pace with the advancing development of the flowers. In capitulate inflorescences the marginal flowers open first, and those in the centre last (see vol. i. p. 740). The flowers of each outer series are therefore always further advanced than those of the adjoining inner series, and when the mature stigmas are already opened in the outer flowers, the pollen of the inner ones is only just being pushed out of the anther-tubes and shaken off the stylar branches as they separate. A wonderful contrivance now meets our gaze—the mature stigmas of the outer flowers are brought directly under the inner flowers so as to catch their pollen as it falls, a condition brought about by the alteration in form of the receptacle on which all the flowers stand. Sometimes the pollen does not need to fall, for the flowers stand so closely side by side and above one another that the divergent stigmas of the older flowers come at once into direct contact with the pollen of the younger flowers. This is the case in various species of the Groundsel genus (*Senecio*) where the two stylar

branches diverge, not in a horizontal but in a vertical plane, the consequence being that one of the stylar branches comes in contact with the clumps of pollen just pushed out from a neighbouring higher flower. Of course there exist among Composite flowers quite a number of forms intermediate between those here described, all of which promote geitonogamy, but we cannot enter upon them further.

Among Umbelliferous plants, as in Compositæ, the numerous small flowers are crowded so closely together that the stigmas and pollen of neighbouring flowers can easily touch and combine, and a glance at these inflorescences is enough to suggest the possibility of geitonogamy. The conjecture is confirmed on a closer scrutiny, for the Umbelliferæ, as a matter of fact, exhibit an even greater variety of contrivances for geitonogamy than do the Compositæ. The most important of these will now be detailed. First, let us examine the group which is typified by the genera *Eryngium* and *Hacquetia*. In these the flowers are crowded together in capitulate masses surrounded by broad conspicuous bracts. They are all hermaphrodite and protogynous. The stamens with closed anthers are bent inwards in each flower like hooks, and the petals are still unfolded, but the sticky, shining stigma on the top of its long style already projects some distance out of the bud. At this stage the stigma can only be pollinated with pollen from other plants, indeed, from other species. Later, the stamen-filaments elongate and straighten, whilst the anthers dehisce, and pollen appears through the clefts. This pollen comes into contact either at once or very soon with the still receptive stigmas; for the long styles have meanwhile inclined more to the side, so that their stigmas are placed in such a position with regard to neighbouring flowers that either they brush against the pollen-covered anthers, or else are pollinated with the crumbling pollen which falls from these anthers.

The genera *Sanicula*, *Astrantia*, and *Laserpitium*, differ somewhat from this group of Umbelliferæ. The chief modification is that in the species of these three genera staminate as well as hermaphrodite flowers occur. In *Sanicula* each umbel consists of 3 true hermaphrodite flowers in the centre, and 8-10 staminate flowers arranged round them like a wreath. The hermaphrodite flowers are protogynous and the first to develop, so that at the beginning of flowering the stigmas can only be fertilized with the pollen from plants of other species. The stamens straighten afterwards and project like the style far out of the flowers. But the anthers and stigmas of the same flowers do not touch, since the styles stand up erect, whilst the stamens have an oblique direction. A crossing soon takes place, however, between the hermaphrodite flowers and the adjoining staminate flowers, in the following way. The stamens of the hermaphrodite flowers wither and fall off, and the stigmas of these flowers become divergent, curving slightly outwards, so that their still receptive surfaces are brought into the surrounding circle of stamens. The anthers of the male flowers have meanwhile dehisced and are shedding abundant pollen. The stigmas are necessarily pollinated either by the direct contact of stigmas and anthers, or, by the falling of the pollen from these anthers. The arrangement of the flowers in *Astrantia* has already been described on p. 296; it



agrees with *Sanicula* in having hermaphrodite and staminate flowers in each umbel, the hermaphrodite flowers developing first and being protogynous, so that again the sticky stigmas of the first-opened flowers in a given locality can only be fertilized by the pollen of other species. Later, the stigmas of the hermaphrodite flowers separate, and to a certain extent offer themselves to the pollen of the neighbouring staminate flowers which is now being shed. *Laserpitium* exhibits the same general arrangement of flowers as *Sanicula* and *Astrantia*, but the hermaphrodite flowers in the large, loose umbel are protandrous instead of protogynous. Geitonogamy, however, obtains, just as in *Astrantia*, by the stigmas at the top of the divided style exposing themselves to the pollen from the anthers of the neighbouring staminate flowers. Since the protandrous hermaphrodite flowers open before the staminate ones, their stigmas are mature exactly at the same time that the anthers of the latter shed their pollen.

A notable exception to these Umbelliferae which have been described, where the stigmas of one flower obtain the pollen from neighbouring flowers by the elongation and bending of their styles into their neighbour's domain, thus producing geitonogamy, is afforded by others whose styles and stigmas retain their original position. The stamens, however, elongate and straighten, and assume such a position that the pollen liberated from their anthers can reach the stigmas of the neighbouring flowers. One group of such species, of which *Pachypleurum*, so abundant on the mountain heights of Europe, may serve as a type, develops a single flat umbel at the end of the stalk bearing flowers all hermaphrodite. They are also protogynous—their sticky stigmas can receive pollen, while their anthers are still closed. When flowering first begins, therefore, crossing can only be with other plants. Then the stamens straighten and stand out on all sides like a star till the long filaments place their anthers in the line of the neighbouring flowers. Since the stigmas are still receptive some of the pollen falling out of the bursting anthers inevitably reaches the stigmas of one of these flowers. The process which occurs in the umbel of *Siler* is but slightly different, although the flowers are exclusively protandrous, and not protogynous like those of *Pachypleurum*. In spite of this difference in the times of maturation the end attained is the same, as we shall see. The flowers in an umbel of *Siler* do not mature simultaneously like those of *Pachypleurum*, but the development proceeds very gradually from the circumference towards the centre of the umbel, so that the anthers of the central flowers do not dehisce until the outer ones have lost their pollen and matured their stigmas. Some of the crumbling pollen which falls out of the shrivelling anthers is now deposited on these ripening stigmas, since the thread-like filaments are long enough to reach to the middle of the outer flowers, and thus geitonogamy almost invariably ensues.

Both *Pachypleurum* and *Siler* and all the Umbelliferae typified by them contain only hermaphrodite flowers in their umbels, and in this respect they differ from species of *Athamanta*, Spiguel (*Mewm*), and Chervil (*Chærophyllum*, see figs. 294<sup>3</sup> and 294<sup>4</sup>, p. 320), whose umbels contain both hermaphrodite and staminate flowers like those of *Astrantia* and *Sanicula*. But this arrangement of the

flowers causes no alteration in the process of fertilization described. We would merely observe that in these plants the hermaphrodite flowers always open earlier than the staminate flowers of the same umbel. Not until the stamens of the hermaphrodite flowers have dehisced and fallen away, whilst their stigmas have been waiting for two days for pollen from other plants, do the anthers of the staminate flowers open after growing up far beyond their corollas. Their pollen then falls on the stigmas of the hermaphrodite flowers. Since there are so many more staminate than hermaphrodite flowers, the success of the process is doubly assured. For example, the umbel of *Chærophyllum aromaticum* (see figs. 294<sup>3</sup> and 294<sup>4</sup>) contains 20 staminate flowers besides one central and 3-5 peripheral hermaphrodite flowers, and therefore to 8-12 functional stigmas there are about 100 anthers. Moreover, the hermaphrodite flowers in these Umbelliferae assume such a position at the moment the staminate flowers open that a pollination of their stigmas by the falling pollen is almost unavoidable (fig. 294<sup>4</sup>).

One of the most remarkable instances of geitonogamy is observed in such Umbelliferae as the Beaked Parsley (*Anthriscus*), Fennel (*Fœniculum*), Coriander (*Coriandrum*), Water Parsnip (*Sium*), and *Ferulago*. All the species of these genera have two kinds of inflorescence. The umbels which blossom first contain principally true hermaphrodite flowers with a few isolated staminate flowers here and there; the later umbels consist only of staminate flowers. The hermaphrodite flowers which come first are completely protandrous; the anthers, borne on very thin filaments, are brought one after the other to the centre of the flower, where they dehisce and scatter their pollen, and the day following they drop off. After all the five stamens have dropped off the stigmas become mature and receptive. They continue in this condition for two days, and during this period are liable to crossing with the pollen of other plants. Then the umbels bearing only staminate flowers come under consideration. The pedicels which bear them have meanwhile elongated, and have thus obtained such a position that these umbels stand right over the hermaphrodite flowers with their mature stigmas, so that they seem to form an upper story, so to speak, in the inflorescence as a whole. Now, when the anthers in the staminate flowers of this upper story open, and when their walls shrivel up, the pollen is thrown out and falls vertically downwards in minute crumbling masses. The stigmas of the lower, older flowers are thus subjected to a rain of pollen, and it is easy to see that the majority of the stigmas are pollinated in this manner.

The instances of geitonogamy described in Compositæ and Umbelliferae may be regarded as typical of what occurs in many representatives of other families. The Stellatæ section of Rubiaceæ, Caprifoliaceæ, Cornaceæ, Scrophulariaceæ, Rosaceæ, Polygonaceæ, Liliaceæ, and Aroideæ, whose flowers are crowded together in capitula, balls, fascicles, spikes, and racemes, repeat these processes sometimes down to the minutest detail. For example, the two styles in the protandrous fascicled flowers of a Woodruff, *Asperula taurina*, elongate, separate from each other and bend over just like those of *Laserpitium*; by this alteration of position they get into the

region of the younger flowers, where pollen is being shed, and their stigmas thus actually come into contact with the pollen. The process is still further promoted in this species of Woodruff by the fact that the last flowers to be produced are staminate. In the Red-berried Elder (*Sambucus racemosa*), various species of the Cornel and Dogwood genus (*Cornus florida*, *mas*, *sanguinea*), in the Vines (*Vitis*), which bear true hermaphrodite flowers, in the Tufted Loosestrife (*Lysimachia thyrsoflora*), and in many Spiræas (*Spiræa*), the arrangements for geitonogamy resemble those of *Siler trilobum* in that the direction of the style and the position of the stigma remain unaltered, but the filaments of the anthers elongate and bend over so as to deposit the pollen on the stigmas of adjacent flowers. In the Way-faring-tree and Guelder-rose (*Viburnum Lantana*, *V. Opulus*) we have yet another contrivance—the pollen which is shed from the bent anthers of one flower falls to the bottom of the cup-shaped corolla of an adjacent one, where the large cushion-like stigma is situated.

The process of geitonogamy in the Snake-root (*Calla palustris*) and in *Saxifraga juniperifolia* to some extent resembles the fall of pollen in Compositæ. The flowers in these plants are crowded in short spikes or fascicles. They are protogynous, the stigma in the lower half of the inflorescence not ripening until the upper flowers are shedding their pollen. Now, when the anthers begin to shrivel and the pollen is thrown out, it necessarily falls on the fertile stigmas below. In those species of *Veronica* which have spicate inflorescences (*Veronica maritima*, *spicata*, *spuria*, &c.), the method of geitonogamy is slightly different, for here the style undergoes peculiar movements during the flowering period. The crowded flowers are all protogynous, and the stigmas of the flowers which first unfold are exposed to the pollen of plants of other species. This continues for two days. Meanwhile the stamens of the lowest flowers on the spike have elongated and pushed their anthers into the place first occupied by their stigmas; the anthers then dehisce and shed their pollen. But shortly before this the style has bent sharply downwards so that it is impossible for its stigmas to come in contact with this liberated pollen. Not until all the pollen has fallen down by the shrivelling up of the anthers or has been carried away by insects do the styles again straighten and project almost horizontally from the axis of the spike. The upper flowers on the spike undergo the same course of development, but the stages here are two days later. On this account the pollen falls from the anthers of the higher flowers just when the styles of the lower flowers again become straight. The still fresh stigmas at the ends of the styles thus come into line with the falling pollen and are efficiently pollinated by it.

A similar process occurs in *Eremurus* (see fig. 293<sup>2</sup>, p. 309), but here there is no fall of pollen. The stigmas at the end of the just straightened style are brought by their change of position directly into contact with the orange-yellow pollen still clinging to the withered anthers of the higher flowers. Many of the styles, of course, brush by the anthers without effecting this contact, and accordingly many stigmas in the racemes of *Eremurus* remain unpollinated. The transfer of the



pollen by insects occurs but seldom in this plant, so that from the many ovaries in the inflorescence of *Eremurus* usually only a few fruits are matured. This is the more remarkable as these flowers have remarkably long-lived stigmas, a peculiarity which is generally very advantageous in bringing about cross-pollination. The stigma is already mature when the perianth opens; when the tips of the perianth roll back and assume the form of aphides (see p. 171), and when the style moves like the hand of a watch towards the axis of the inflorescence, the stigma is still receptive, and remains so even when the style has again straightened and assumed an oblique upward direction.

A peculiar instance of geitonogamy is observed in *Allium Victorialis*. Each umbel is composed of flowers of very different ages. Before the first flowers bend over, wither, and shrivel up, their pollen-covered anthers project well over the edge of the perianth. In the younger flowers, at the same time, the anthers are still closed and covered by the perianth-leaves, but the stigmas are ripe and project beyond them. These young and hitherto short-stalked flowers are now raised by the elongation of their pedicels and inserted between the older flowers, so that, as a matter of course, their stigmas are brushed by the pollen of the older flowers, if it does not indeed fall on them.

The geitonogamy in the Bistort (*Polygonum Bistorta*) is very strange. It is rendered rather complex, as a peculiar distribution of the sexes is combined with a pronounced dichogamy and a peculiar way of opening. The inflorescence, which looks like a spike, is really composed of numbers of tiny two-flowered groups crowded together. One of the two flowers of each little group is long-styled and truly hermaphrodite, while the other contains a short style, well-formed stamens, and a rudimentary ovary which develops no further. It is therefore a pseudo-hermaphrodite staminate flower. In each group the long-styled hermaphrodite flower opens first, beginning at the base of the apparent spike and gradually working up to the top. The staminate flowers do not get their turn until the highest of the long-styled flowers has opened; but after this they behave exactly like their neighbours, *i.e.* the lowest develops first. The long-styled flowers are protandrous. At the commencement of flowering the pollen-covered anthers project a millimetre from the perianth; the styles, however, are still short and hidden in the interior. At this time pollen can only be removed from the flowers. Then the anthers fall off and the styles elongate so as to protrude some 3 mm. beyond the perianth. The whole spike is at this stage beset with receptive stigmas which can only be fertilized by insects with pollen from other plants. But this state of things does not last long, for now the staminate flowers open one after another in quick succession. Their anthers, containing abundance of pollen, protrude 3 mm. beyond the perianth and come into contact with the still receptive stigmas of their neighbours, so that geitonogamy results. As soon as this is effected the staminate flowers become detached from the axis of the spike and fall to the ground. This geitonogamy is of course useless to the stigmas which have already received pollen from other plants by insect agency, but it is of the greatest importance to the flowers

which have not been so visited, for they would otherwise wither without being pollinated. In this sense we may regard the staminate flowers of *Polygonum Bistorta* as reserve flowers which, in case of absence of insect-visits, can come to the rescue in the last extremity with their own pollen.

Many plants related to the Bistort belonging to the Rhubarb and Dock genera (*Rheum*, *Rumex*), and many species of the Meadow-rue (*Thalictrum*) belonging to the Ranunculaceæ, agree for the most part with the case just described. The hermaphrodite flowers of the Rhubarb are protandrous. The anthers project, one after the other, above the edge of the tiny bell-shaped perianth, where they open and emit their floury pollen. This is easily shaken off by the least movement, and soon afterwards the anthers tumble off their filaments. At this time the three styles on the top of the ovary are bent back, and the large, swollen, cauliflower-like stigmas are so hidden at the base of the perianth that the pollen can gain no access to them. Not until all the anthers have fallen off do the styles straighten and place their succulent three-lobed stigmas in front of the edge of the perianth. Since the development of the extensive inflorescences of the Rhubarb takes place only gradually, one flower withering when another near it has just opened, the pollen shaken from the anthers of the younger flowers usually falls on the stigmas of the older ones. Sometimes the pseudo-hermaphrodite staminate flowers, which also occur in the inflorescence of the Rhubarb, and which are the last to open, have to provide the pollen for the adjoining hermaphrodite flowers, and after having performed their task they fall off. The course of development in the Alpine Dock (*Rumex alpinus*) gives rise to geitonogamy, but the process differs from that in the Rhubarb, since the stigmas do not emerge from their hiding-place in the depths of the perianth by the straightening of the style, but are rendered conspicuous by the folding back of the perianth-leaves, whilst in several Meadow-rues (*Thalictrum alpinum*, *fætidum*, and *minus*) the stigmas, which are at first concealed under the petaline sepals, are exposed and rendered accessible to the pollen of neighbouring flowers by the falling away of the sepals which cover them.

These plants have floury pollen which, in the absence of wind, may fall vertically on the stigmas of neighbouring flowers, but whose transport is usually effected by breezes. They therefore afford a transition to such plants as have hermaphrodite flowers in which geitonogamy is chiefly brought about by the wind, although it may also result in the same way as in the Meadow-rues and the Docks and Rhubarbs. These plants were mentioned when we were considering the inadvisability of dividing plants into those which are respectively anemophilous and entomophilous (see p. 129). These plants would belong to both classes; at first they are insect-fertilized, and later on they are fertilized by the wind. The Mediterranean Heath (*Erica carnea*), which grows in Alpine districts from the valley-floor almost to the summits of limestone mountains, may be taken as the type of some two hundred Ericaceæ. This plant is much frequented by bees, and their visits are the cause of manifold crossings, sometimes between the flowers of the same plant, sometimes with other plants. In this plant, however, the crossing of neighbouring

flowers is more often effected by the wind. This process will be rendered clearer with the help of figs. 295<sup>1, 2, 3, 4</sup>. The flowers are arranged in a row, with their mouths directed to one side pointing obliquely downwards (295<sup>1</sup>). Flowering begins at the top of the branch, and then works gradually downwards. The stigma comes into sight simultaneously with the opening of the corolla, and protrudes some distance in front of its mouth by the elongation of the style. The anthers surrounding the style are still closed, and are either wholly or half hidden in the corolla (295<sup>2</sup>). Bees coming to suck the honey at the base of the flower inevitably

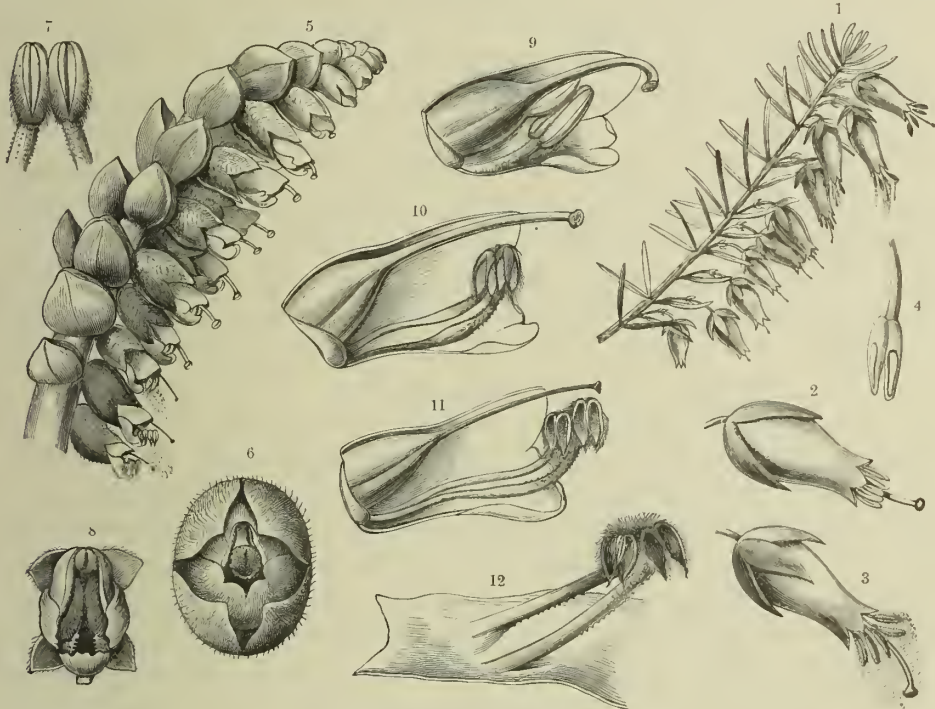


Fig. 295.—Geitonogamy with dust-like pollen.

<sup>1</sup> *Erica carnea*; branch with flowers on one side only. <sup>2</sup> Flower of the same in its first stage. <sup>3</sup> The same flower in its last stage. <sup>4</sup> Single stamen of *Erica carnea*. <sup>5</sup> *Lathraea Squamaria*; upper part of inflorescence. <sup>6</sup> Front view of a flower which has just opened. <sup>7</sup> Two anthers with closed loculi from the same flower. <sup>8</sup> Front view of a flower at a later stage. <sup>9, 10, 11</sup> Longitudinal sections of three flowers in the first, second, and third stages respectively. <sup>12</sup> Two anthers whose floury pollen has fallen, leaving empty loculi. <sup>1</sup> and <sup>5</sup> nat. size; the others somewhat enlarged.

brush against the stigma in consequence of its peculiar position. If they have brought pollen with them from other Heaths, a crossing between different plants is the result. Meanwhile large pores have formed in the anthers (see fig. 295<sup>4</sup>). But since the pores on adjacent anthers are in immediate contact with one another, and since the anthers themselves are held together by the corolla (which is rather constricted at its mouth), as if by a ring, the pollen remains stored up in the anther-cavities and the pollen-tetrads do not fall out unless disturbed in some way. The anthers are disturbed whenever a bee inserts its proboscis into the flower in search of the honey, and therefore the same bee which at first brushed against the project-



ing stigma is, in the next instant, smothered in pollen over its proboscis, head, and thorax. Cross-pollination must ensue if this bee shortly after visits the flowers of another plant, and wherever Heaths which flower simultaneously grow together there is no lack of hybridization. Whether the stigma of a flower is pollinated by bees with pollen of another plant of the same or of another species or not at all, it always begins to wither in two days' time and ceases to be receptive. The stamens in the same flower now elongate and push their anthers out of the corolla mouth. The restriction being removed the anthers separate, and pollen will fall out of their compartments at the slightest movement (see fig. 295<sup>3</sup>). The merest swaying of the flowering branch is sufficient to cause the pollen to fall. The still receptive sticky stigmas of the younger flowers on the same branch, and indeed of flowers on other branches of the same plant at some distance, are thus necessarily pollinated with the dust-like pollen.

In the inflorescence of the Toothwort (*Lathræa Squamaria*) the crossing is effected in exactly the same way. The flowers, like those of the Heath, are all turned towards the side from which insects may be expected to arrive (see fig. 295<sup>5</sup>). They are protogynous, and the ripe stigma projects beyond the margin of the corolla before the latter has properly opened and when the anthers below are still closed (see figs. 295<sup>6, 7, 9</sup>). At this stage the stigma can only be pollinated with the pollen of other plants whose development is further advanced. Corolla, style, and filaments continue to elongate, the style, which has hitherto been bent like a hook, straightens, the stigma, which was formerly in front of the narrow entrance to the flower, takes a higher position, the anthers dehisce, and the flower now enters upon its second stage (see figs. 295<sup>8</sup> and 295<sup>10</sup>). Pollination is effected at this time by insects. Humble-bees suck the honey secreted by a succulent cushion below the ovary, and so transfer the pollen of the Toothwort from flower to flower. When they come to a flower they brush against the projecting stigma and deposit pollen on it which they have gathered elsewhere; they then push their probosces between the anthers, which are held together by soft hairs. They are obliged to take this path, for otherwise they would soon come to grief. The filaments below the anthers are studded with little pointed thorns (see fig. 295<sup>10</sup>), and the humble-bee carefully avoids any contact with them. He therefore passes between the contiguous anthers of the sprinkling stamens (*cf.* p. 271), separating them slightly, and thus causing a fall of dusty pollen which covers his proboscis and head. And now comes the third and last stage. The style and stigma wither and dry up, and the stamens elongate and push their anthers beyond the margin of the corolla (see figs. 295<sup>11</sup> and 295<sup>12</sup>). The anthers no longer cohere. The pollen retained in their cavities is carried away by the wind, and will be deposited in part on the still receptive stigmas of neighbouring, younger flowers. If a flower has already been visited by a humble-bee very little pollen will remain in its anthers, but if there has been no insect-visit the anthers are full of pollen when they are extended from the flower, and this is wafted in small clouds to the stigmas of the younger flowers in the upper part of the spike. Here again, as in so many instances, geitonogamy does not supervene till towards

the close of flowering. At first the plant seems to offer facilities for hybridization, later for a crossing of different plants of the same species, and not until both these processes have failed, owing to lack of insect-visits, does it fall back on cross-pollination between neighbouring flowers of the same plant. The processes and contrivances in the flowers of *Clandestina rectiflora*, *Bartsia alpina* and of some other Rhinanthaceæ agree in the main with those of the Toothwort, so that there is no need to describe them in detail. In conclusion, the Persian *Crucianella stylosa*, one of the Stellatæ group of the Rubiaceæ, must be considered especially with regard to the geitonogamy of its hermaphrodite flowers. This plant has already been mentioned (pp. 265, 267), and it was stated that the tips of the corolla-lobes formed a hollow cone which at a touch suddenly burst open, scattering the pollen hidden beneath (fig. 272). If an insect is the cause of the disturbance it becomes covered with the liberated pollen, and should it then visit other flowers of this same *Crucianella* it is not too much to say that the pollen it carries on its body will be deposited on the stigmatic tissue at the thickened end of the slender styles projecting far above the corolla (see fig. 272<sup>5</sup>). If the flower is not visited, however, it will burst open and scatter its pollen spontaneously. The dust-like pollen is then diffused into the surrounding air, and so easily reaches the ripe stigmas of the neighbouring flowers.

#### AUTOGAMY.

By the term *Autogamy* is understood the transference of pollen from the stamens to the stigmas of the same flower, in other words—*self-pollination*. Autogamy can, therefore, only occur in hermaphrodite flowers, but it must not be inferred that the only method of reproduction in hermaphrodite flowers is by autogamy. In the last chapter we showed the error into which Linnæus fell by making this assumption, and referred to the almost interminable list of contrivances to bring about cross-pollination in hermaphrodite flowers between different species, between different individuals of the same species, and between flowers on the same individual. This important result of modern investigation has led not only to a correction of the views of the celebrated Swedish Botanist, but to the belief that autogamy is avoided in the vegetable world. Darwin even held the opinion that there must be something injurious in autogamy to account for the number of obstacles placed in its way. This statement, though commonly made in text-books as embodying a law of nature, is, however, not a correct expression of the facts observed. It is true that cross-pollination appears to be the primary object aimed at, but it is not true that autogamy is avoided. If cross-pollination takes place there is naturally no necessity for subsequent autogamy, but if cross-pollination fails autogamy assumes an importance of its own, and the contrivances which have been observed to bring about autogamy are no less numerous than those which favour cross-pollination. That flowers should be adapted at different times to two such diverse purposes as cross- and self-pollination is one of the marvels of floral construction.

As the above conclusion forms the main basis of the theory concerning the origin of species to be presently unfolded, some preliminary account of the observations on which it is founded must now be given, but the task is not an easy one. For five-and-twenty years I have been studying, with special reference to the phenomena in question, the flowers of many more than a thousand species in all stages of development from budding to fruiting, some growing wild in their original habitats, some in the Gardens under my direction, and my notes are so numerous that even the briefest outline of the cases observed would fill several volumes. I must, therefore, content myself with presenting the different instances in groups according to their degrees of similarity. Even the number of groups, however, is surprisingly large, and only their general description can be attempted. The best way will be to select a representative species for each kind of adaptation that we have to deal with, and to point out in a few words its more important characteristics. As the processes to be described as taking place during the flowering period all tend to the same result though differing greatly in other ways, and as the terms used must be applied over and over again to the phenomena which are common to all the cases, it is impossible to avoid a certain monotony in the descriptions that follow, and the reader is begged to exercise some patience in the perusal of this chapter.

The simplest case of autogamy occurs as follows. The flower opens revealing the stigma stationed in front of the entrance to the receptacle and already mature, whilst the anthers are closely adherent to the stigma but are still closed. Autogamy is, for the time, impossible, whereas cross-pollination may be effected through the intervention of wind or insects. In the second half of the flowering-period the anthers adjacent to the stigma open, and the stigma is instantly covered with the pollen set free from them. There are only a few varieties of this simplest case of autogamy worth mentioning. It has been observed to occur in particular in annual plants with small flowers (e.g. *Centunculus minimus*, *Geranium pusillum*, *Lithospermum arvense*), and again in several bulbous plants belonging to the section of Lilifloresæ, e.g. several species of *Fritillaria* and *Narcissus*, all the species of *Trillium* and *Uvularia*, and in a few species of *Crocus*. In *Trillium grandiflorum* and *Uvularia grandiflora*, two anthers are stationed in each of the three angles of the spreading stigmas, and in the process of autogamy only the pollen from that half of the anther which is turned inwards is used, whilst the pollen from the outward-facing halves of the anthers may be carried away by insects, even after autogamy has taken place. In the Crown Imperial (*Fritillaria imperialis*) only the pollen from the three longer stamens falls upon the stigma of the same flower. There are six stamens in the flowers of this plant, three of which are longer than the rest and alone have their anthers appressed to the tridentate stigma. These anthers open a day later than the others. Dehiscence is accompanied by a very considerable shrivelling and shortening of the anthers, and the result of this contraction is that the liberated pollen is scraped off the anthers by the edges of the stigmatic lobes. In *Crocus albiflorus*, which covers alpine meadows in early spring with its blossoms, the anthers at first rest with their arched backs in



contact with the stigma. The loculi, full of adhesive pollen, face outwards, and are so placed that insects coming in quest of honey must rub off the pollen emerging from their slits. The stigmas, on the other hand, assume such a position that the insects are obliged to touch their receptive tissue before brushing the anthers. Owing to the relative positions of stigmas and anthers cross-pollination is no doubt effected by insects in a large number of cases, and as only the backs of the anthers rest upon the stigma autogamy is, for the time, impossible. But towards the close of the flowering period the anthers are twisted round, with the result that the pollen of each loculus touches the stigma. Another circumstance contributory to this autogamy is that during the time of flowering the perianth-tube elongates from 5 to 15 mm., and the filaments, which are adnate to the perianth, from 3 to 4 mm. The anthers are in consequence pushed past the stigmatic margins and leave more pollen upon them than would otherwise be the case.

*Convolvulus Siculus*, a native of the shores of the Mediterranean, may be taken as a type of several annual Bindweeds wherein the style bifurcates into two narrow filiform branches of considerable length which bear the receptive tissue and represent stigmas. One of these stigmas is erect, and continues the style in a straight line, whilst the other stands away at an angle of  $60^\circ$ , and forms a barrier in front of the approach to the floral receptacle. The stamens are adherent to the style, and at the time that the corolla opens the anthers rest against the erect stigma. At the period of dehiscence the anthers face outwards so that the upright stigma encompassed by them cannot receive their pollen when the flower first opens. On the other hand, the position of the anthers is favourable to the abstraction of pollen by insects seeking the honey in the interior of the flower. Later on, when the anthers shrivel they become covered all over with pollen, and then it is that a portion of it is transferred to the erect stigma, thus effecting autogamy. The second stigma, which lies across the entrance, seldom has pollen from the anthers of the same flower affixed to it; but pollen conveyed from other flowers is rubbed off insects on to this stigma, so that here we have an instance in which one stigma is adapted to autogamy and another to cross-pollination.

The process of autogamy occurs in pendent flowers, the anthers of which are joined together in a central cone, through a relaxation of the filaments towards the close of the flowering period, in consequence of which the loculi full of pollen no longer close together so tightly as before. The mealy pollen falls from the dislocated cone upon the stigma, which is still in a viscid and receptive condition. As types of this category of plants we may take the Snowdrop (*Galanthus*), *Soldanella*, of which previous mention has been made (see fig. 278<sup>1</sup>, p. 275), and *Dodecatheon*, which is allied to *Soldanella*, but in respect of the form of its flowers resembles *Cyclamen*. During the first part of their flowering-period they are adapted to cross-fertilization. The style projects far beyond the cone of anthers. Insects in search of honey begin by brushing against the stigma and then for a moment dislocate the anthers, letting a sprinkling of pollen fall on their heads. On visiting other flowers they rub this pollen on to the stigmas and so promote cross-fertilization. If, however, no insects

visit a flower, the anthers are still full of pollen at the close of its flowering period, and being then displaced let fall their pollen upon the slightest vibration of the pendent blossom, or even when it is quite still. The pollen falls straight down and is caught by the stigma below.

The process above described is only observed to take place in pendent flowers where the pollen is of floury consistency and the stamens are united into a conical cap. Flowers borne on horizontal stalks, and facing sideways, may exhibit the same phenomenon in connection with separate stamens. Only an important circumstance in this case is that some of the anthers should be exactly over the stigmas at the time of dehiscence. With a view to cross-fertilization, lateral flowers of the kind are protogynous, and have their anthers closed when the buds open; but later on the anthers dehisce, and a portion of the pollen then liberated falls out, owing to the contraction of the walls of the anthers, and besprinkles the stigma of the same flower. This method of autogamy has been observed in particular in the flowers of *Tofieldia* and the Bog Asphodel (*Narthecium*).

Even in upright flowers autogamy sometimes takes place in the second half of their time of flowering through a fall of pollen, and that without any change of position on the part of petals, stamens, or style. To make cross-fertilization possible, in the first instance, flowers of this kind are protogynous. Subsequently, after the dehiscence of the anthers, a portion of the crumbly pollen becomes detached, and is deposited on the stigma below. In the case of erect flowers with funnel-shaped corollas, the pollen slips down the smooth sloping wall of the funnel to the stigma, and it is not essential for the anthers to stand vertically above the stigma, since the corolla acts as a sort of conduit for the pollen. The Lilac (*Syringa*) is an example of the plants of this category. It is also remarkable for the fact that, though its flowers are only protogynous for a very short time, yet, for one or two days after the dehiscence of the anthers, autogamy cannot take place, because the anthers face outwards. So long as the anthers are in this position the pollen cannot be transferred without extraneous aid to the corolla-tube; it is not till later on, when the anthers get covered all round with pollen, owing to the gradual shrinkage of their walls, that some of the pollen drops on to the stigma standing underneath in the tube of the funnel.

Very often in erect or obliquely ascending flowers autogamy is brought about by an elongation of the filaments during the period of flowering, the result being that the anthers, which are originally lower down than the stigmas, are elevated to the same level as the latter, and are thus enabled to deposit their pollen upon them. Most of the species belonging to this group are protogynous; the filaments are erect, and are either adherent or else parallel to the ovary or style. At first the anthers are so far from the stigma that the pollen would not of itself dust the stigma in the same flower, but the subsequent elongation of the filaments is so regulated as to carry the anthers to the same level as the stigma by the time they are coated with pollen. The anthers then adhere to the receptive stigmatic tissue, and autogamy is the result. The following are instances of plants

in which this is observed to occur:—the Moschatel (*Adoxa Moschatellina*), most of the species of the Knawel (*Scleranthus*), *Pæderota Bonarota*, of wide distribution in the Southern Alps, the curious *Aponogeton distachyon*, native to South Africa, and a large number of Cruciferae, Saxifragaceae, Willow-herbs, Geraniaceae, Convolvulaceae, and Caryophyllaceae.

Of the large family of the Cruciferae we may mention *Arabis cœrulea*, *Braya alpina*, *Cardamine alpina*, and *Rhizobotrya alpina*, all of which are small-flowered species growing in the upland hollows of high mountains, and in addition the annual or biennial species named *Lepidium campestre*, *L. sativum*, *Sisymbrium Alliaria*, *S. Thalianum*, *Thlaspi alliaceum* and *Thlaspi arvense*. In these plants the stigma is sessile on the ovary in the shape of a small round cushion, which becomes visible the moment the imbricate petals of the bud begin to move apart. At this period only cross-pollination can take place, as all the anthers in the flower itself are still closed; but the four long stamens now grow up along the wall of the ovary until the anthers are exactly on the same level as the stigma. The anthers have dehisced by that time, and their pollen cannot but be deposited on the receptive cells at the periphery of the stigmatic cushion. Another observation which has been repeatedly confirmed, is that only one of the four anthers parts with its pollen to the adjacent stigma, while the rest, though quite close to the stigma, are not in immediate contact with it. The pollen of these three anthers is apparently placed there so that it may be carried off by the small flies which visit these cruciferous plants and transferred by them to younger blossoms.

The Saxifrages (e.g. *Saxifraga androsacea*) here in question have two linear or oblong stigmas. After the anthers are raised, the pollen is usually brushed off them on to the sides of the stigma near its base. But here again it is noteworthy that for the most part only one of the five anthers devotes its pollen to the process of autogamy, whilst the others remain a little below the stigmas, and do not come into contact with them.

In a number of small-flowered Willow-herbs (*Epilobium collinum*, *E. montanum*, *E. parviflorum*, &c.) the stigma is composed of four thickish divergent lobes arranged in a cross with four angles between them. Upon the first parting of the petals, which always happens early in the morning, the anthers may be seen to be underneath the mature cruciform stigma, but in the course of that very day the filiform filaments grow to a sufficient length to place the anthers in the re-entrant angles of the cross. Meanwhile, dehiscence has taken place, and by the evening of the first day autogamy ensues. During the night the petals close up, and the flower droops a little; the next morning the petals open again, and it is then evident that the filaments have grown rather longer, two or three pollen-covered anthers standing above the stigma and partially concealing it. The place occupied by the stigma on the previous day is now filled by an assemblage of anthers laden with pollen, which is brushed off by insects and transported to other flowers. Thus we find in these Willow-herbs that on the first morning cross-fertilization



alone is possible, in the evening of the first day autogamy takes place, and on the next day pollen is again supplied to fertilize younger flowers—an alternation which clearly shows that autogamy is not invariably merely a last stage in the phenomenon of flowering.

Similar events occur in several small-flowered species of the Crane's Bill (e.g. *Geranium columbinum*, *G. lucidum*, *G. Robertianum*). In the middle of the newly-opened flower is a receptive stigma with five radiating arms, and around it are ten stamens, all of which are still closed. Five of the stamens are longer than the rest, and hold their anthers nearly on a level with the stigma; the other five anthers form a belt underneath the stigma. By the evening of the first day the anthers of the longer stamens are already open, and transfer their pollen to the tips of the adjacent stigmatic lobes. In *Geranium lucidum* the phenomenon is not even delayed till the evening, but takes place four hours after the flowers open. The flowers are not, however, then over. They close for the night, and nod or droop to protect the pollen (see figs. 225<sup>1</sup> and 225<sup>2</sup>, p. 121), but next morning they again become erect. The five stamens standing in front of the petals then grow until the anthers reach the niches between the radiating lobes of the stigma, whereupon there is a transference of pollen to these lobes. Some of the anthers are afterwards lifted still higher, evidently for the purpose of dispersing, by aid of insects, such portion of the pollen as has not been applied to the process of autogamy.

Several Convolvulaceæ, of which the well-known *Ipomœa purpurea* is a type, have only two or three of their five stamens adapted to autogamy. The stamens, which are parallel to the style and usually adherent to it, are of unequal length, the shortest being 9 mm., the longest 17 mm., and the others 11 mm., 13 mm., and 15 mm. in length respectively. The anthers consequently stand at different heights and at the same time they are so disposed relatively as not to cover one another, an arrangement which has the advantage of presenting a comparatively large expanse of pollen along the passage leading to the honey in the interior of the flower. But even the anther of the longest stamen is 3 mm. lower than the stigma when the flower first opens. Owing to this arrangement and to the circumstance that the flowers are protogynous, only cross-fertilization through the intervention of insects can take place at the commencement of their flowering period. Later on, however, there is a lengthening of the stamens and the anthers pertaining to the longest two or three reach the same level as the stigma, and yield up their pollen to it. The process of autogamy is further facilitated by the involution of the corolla, which occurs at the close of flowering, whereby the anthers coated with pollen are pressed against the stigma.

From these Convolvulaceæ we pass to a long series of protandrous Caryophyllaceæ, mostly annual plants, such as *Agrostemma Githago*, *Saponaria Vaccaria*, and *Silene conica*, in which the anthers are brought into contact with the stigmas by a similar elongation of the stamens. The various changes occurring in flowers of the kind ensue with great regularity as follows:—(1) The petals separate, leaving











